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BATS OF SAINT VINCENT, LESSER ANTILLES



*GARY G. KWIECINSKI, SCOTT C. PEDERSEN, HUGH H. GENOWAYS, PETER A. LARSEN,
ROXANNE J. LARSEN, JUSTIN D. HOFFMAN, FITZROY SPRINGER, CARLETON J. PHILLIPS,
AND ROBERT J. BAKER*

Front cover: Bats of the island of Saint Vincent (from upper left to lower right): (Row 1) *Noctilio leporinus*, *Pteronotus fuscus*, *Micronycteris buriri* (endemic to St. Vincent); (Row 2) *Brachyphylla cavernarum*, *Monophyllus plethodon*, *Artibeus lituratus*; (Row 3) *Glossophaga longirostris*, *Artibeus schwartzi*, *Molossus molossus*; (Row 4) *Ardops nichollsi* (a subspecies endemic to St. Vincent), *Sturnira paulsoni* (a subspecies endemic to St. Vincent), *Tadarida brasiliensis*. Photographs by Gary G. Kwiecinski and Peter A. Larsen.

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BATS OF SAINT VINCENT, LESSER ANTILLES

GARY G. KWIECINSKI, SCOTT C. PEDERSEN, HUGH H. GENOWAYS, PETER A. LARSEN, ROXANNE J. LARSEN, JUSTIN D. HOFFMAN, FITZROY SPRINGER, CARLETON J. PHILLIPS, AND ROBERT J. BAKER

ABSTRACT

The chiropteran fauna of the island of Saint Vincent, represented by 12 species, is among the most complex in the Lesser Antilles, being represented by four families including Noctilionidae (1 species), Mormoopidae (1), Phyllostomidae (8), and Molossidae (2). This fauna includes four trophic guilds as represented by *Noctilio leporinus* (piscivore/insectivore); *Glossophaga longirostris* and *Monophyllus plethodon* (nectarivore/pollenivore); *Artibeus lituratus*, *A. schwartzi*, *Brachyphylla cavernarum*, *Ardops nichollsi*, and *Sturnira paulsoni* (frugivore); and *Pteronotus fuscus*, *Micronycteris buriri*, *Molossus molossus*, and *Tadarida brasiliensis* (insectivore). One species—*Micronycteris buriri*—and two subspecies—*Sturnira paulsoni paulsoni* and *Ardops nichollsi vincentensis*—are endemic to the island. Recent advancements in population genomics have led to the discovery of the reticulated evolutionary history of *Artibeus schwartzi* and it is likely that the formation of the hybrid evolutionary trajectory of this species is linked with classical island biogeography. The bat fauna of St. Vincent is unique in the West Indies, characterized by being a crossroads for species, an outpost for both northern and southern species, the boundary for a multi-island bat fauna as marked by Koopman's Line, and a site of endemism. Based on our studies, we place the bat fauna of St. Vincent as the southern-most island in the Lesser Antillean Faunal Core.

Key words: adaptability, biogeography, Caribbean Sea, Chiroptera, habitat, Koopman's Line, Lesser Antilles, reproduction, reticulate evolution, St. Vincent, species richness, systematics

INTRODUCTION

Islands are crucibles of evolution (MacArthur and Wilson 1967; Whittaker 1998, 2000), which is the reason biologists of all stripes are interested in studying island faunas. The Caribbean islands are among the most studied examples of the interplay among island faunas, dispersal to and from islands and mainland, and evolution of small populations in isolation (Scott 1972; Baker and Genoways 1978; Wright 1981; Hedges 1996, 2006; Davies and Smith 1998; Ricklefs and Lovette 1999; Trejo-Torres and Ackerman 2001; Dávalos 2004, 2005, 2006; Ricklefs and Bermingham 2004a, 2004b; Santiago-Valentin and Olmstead 2004; Willig et al. 2009; Dávalos and Russell 2012; Lamas et al. 2014). Faunal summaries, such as this one on the bats of St. Vincent, serve as the cornerstones for all types of research, help put important data into the scientific

domain, and can be sources of new hypotheses. As it happens, St. Vincent is not just another island in the chain known as the Lesser Antilles. Instead, its geographic location and physiographic features combine to give it a special role in the biogeography and evolution of a number of Neotropical faunal groups (Seutin et al. 1994; Bermingham et al. 1996; Davies and Bermingham 2002; Wilder and Hollocher 2003; Genoways et al. 2010). Perhaps the strongest evidence of the importance of St. Vincent, with respect to Caribbean bat biogeography, is that it resides immediately north of Koopman's line (a geographic feature that defines the distribution of several Caribbean endemics and South American invaders) and it hosts a species of bat that likely originated through reticulate evolution (P. Larsen et al. 2010).

Our goal in pulling together historical and traditional information about the bats known to inhabit St. Vincent was to draw more attention to the island fauna and to be a cornerstone for new research. The chiropteran fauna of the island of St. Vincent, represented by 12 species, is among the more complex in the Lesser Antilles, being represented by four families including Noctilionidae (1 species), Mormoopidae (1), Phyllostomidae (8), and Molossidae (2). This fauna includes four trophic guilds as represented by *Noctilio leporinus* (piscivore/insectivore); *Glossophaga longirostris* and *Monophyllus plethodon* (nectarivore/pollenivore); *Artibeus lituratus*, *A. schwartzi*, *Brachyphylla cavernarum*, *Ardops nichollsi*, and *Sturnira paulsoni* (frugivore); and *Pteronotus fuscus*, *Micronycteris buriri*, *Molossus molossus*, and *Tadarida brasiliensis* (insectivore). The frugivore and insectivore guilds dominate the bat fauna on St. Vincent, but the island appears to lack the aerial insect gleaners found in northern and central Lesser Antillean islands and Barbados.

Although this is an important chiropteran fauna with respect to the Caribbean, it has drawn little attention in the past. The first report was the early description by Gray (1834) of the Antillean fruit bat *B. cavernarum* from caves on St. Vincent. Other records of bats from St. Vincent have been scattered in publications on larger topics, by such authors as Dobson (1878), Andersen (1908), G. M. Allen (1908, 1911), Jones and Schwartz (1967), and Koopman (1968). During the 1950s and 1960s, Albert Schwartz and his field teams collected bats coincidental to their studies on the herpetofauna of the West Indies. These collections resulted in the obtaining of specimens of four species from St. Vincent (Timm and Genoways 2003). In August 1967, J. Knox Jones, Jr., and Carleton J. Phillips made collections at three sites on St. Vincent, including the first record of *A. lituratus* (Jones and Phillips 1970; Jones 1978). Phillips and a research team from the Carnegie Museum of Natural History collected bats between 24 May to 3 June 1986 on St. Vincent as part of ongoing studies of the genetics of the *A. jamaicensis-schwartzi* complex (Pumo et al. 1988, 1996; Phillips et al. 1989, 1991). Finally, in mid-July 1989, Phillips along with Scott Pedersen collected at two sites in St. George Parish to continue studies of the *Artibeus* population of the islands.

Prior to our research, the most extensive field studies concerning bats on St. Vincent were conducted by Nancy Vaughan when she netted bats at 14 sites on 14 nights from 1 to 15 January 1994. Her ecological studies involved a comparison of the chiropteran faunas of seven banana plantations and seven primary or secondary rain forest sites. One of the major results of her research was the discovery of three species of bats previously unknown from St. Vincent—*P. parnellii* [= *fuscus*], *M. megalotis* [= *buriri*], and *T. brasiliensis* (Vaughan 1995; Vaughan and Hill 1996; Vaughan Jennings et al. 2004). Our two mist-netting surveys were conducted over 25 nights during two periods—24 July to 6 August 2005 (12 nights) and 23 May to 8 June 2006 (13 nights). We also explored and sampled 11 day roosts—caves ($n = 6$) and man-made structures ($n = 5$). We captured all 12 species previously reported from the island, which allowed us to develop a greater understanding of the natural history of bats on St. Vincent (P. Larsen et al. 2007, 2010, 2011).

St. Vincent's rugged interior and relatively small size made the island unattractive for the development of large-scale, plantation agriculture during the decades when sugar cane dominated West Indian landscapes. Smaller estates, reflecting a diversity of agricultural efforts, were prominent in the 17th and 18th centuries. Sugar cane became the dominant crop late in the 18th century when planters from neighboring islands began to settle in large numbers. By the end of the 19th century, the sugar cane industry suffered the double blows of a devastating hurricane (1898) and a volcanic eruption (1902), which drove white European planters from the island and precipitated the island's shift from cane to arrowroot production. Currently, the economy of St. Vincent includes agriculture (primary crops: bananas, coconuts, cocoa, root crops, citrus, mangos), tourism, fisheries, and a minor manufacturing sector (Caribbean Conservation Association 1991).

St. Vincent (389 square km; 29 km long, 18 km wide) is located in the southern Lesser Antilles inner arc, an intra-oceanic arc that is approximately a 750-km long chain of active volcanic islands from Saba to Grenada (Caribbean Conservation Association 1991). The climate is humid tropical marine and is affected by the subtropical anticyclone belt and the inter-tropical

convergence zone, yielding a marked seasonality. Rains tend to be showery and distributed roughly into a drier season January to May and a wetter season June to December.

In terms of bats, St. Vincent occupies an important zoogeographic position in the Caribbean as the southern-most boundary of the West Indian Subregion (of the Neotropical Region) described as Koopman's line by Genoways et al. (1998). South of Koopman's Line is an attenuated South American chiropteran fauna lacking any of the Antillean endemic species. Genoways et al. (2010) placed Koopman's line at the 14 km wide Bequia Channel separating St. Vincent and Bequia, the northern-most of the Grenadine Islands. Koopman's line demarks a speciation barrier (physio-

geographically), which is reflected, for example, in limited *Anolis* lizard diversity on St. Vincent, where island bank area and number of colonizing events determines phylogenetic diversity (Helmus and Ives 2013). In birds this line was termed Bond's Line by Lack (1976) and Wunderle (1985), but occurs between Tobago and Grenada.

Additionally, like so many of the islands in the Lesser Antilles, St. Vincent is experiencing economic development that threatens the environment and wildlife, further adding to natural stressors such as hurricanes, volcanic eruptions, and earthquakes. These threats drive the need to document the natural fauna and mitigate the impact of human development.

MATERIALS AND METHODS

Geophysical description of the study area.—The Lesser Antilles is a Cenozoic arc, having formed where the Atlantic seafloor of the South American plate subducts under the Caribbean plate (MacDonald et al. 2000). A single line of islands (Fig. 1) extends from Martinique to northeastern South America (Martinique, St. Lucia, St. Vincent, Grenadines, Grenada, but excluding Barbados) and most of these islands probably emerged in the Oligocene to early Miocene (Speed et al. 1993; Graham 2003). These islands take the form of an arc separated by channels of deep water, such as the St. Vincent Passage (depth of 1,400 m), which separates St. Vincent and St. Lucia (Beard 1949). Physiographically, St. Vincent is separated from the Grenadine Islands at its southern end by the Bequia Channel (depth 1,100 m). The nation of St. Vincent and Grenadines is politically composed of the geographic northern islands of the Grenadines (north of the Petite Martinique Channel), while the Grenadine islands south of the channel are politically adjoined with Grenada. The Grenadines are united along the platform known as the Grenada Bank and were united with Grenada to form a single island during the Last Glacial Maximum (Fig. 2; 26,500 to 19,000 years before present; Clark et al. 2009).

Geologically, St. Vincent has a high ridge never less than 610 m that runs irregularly down the middle of the island. This ridge rises sharply from the sea in

the south to Mount St. Andrew (740 m), runs slightly east of north through Grand Bonhomme (975 m) to the Morne Garu Mountains and Richmond Peak (1,075 m). Here a deep trough runs across the island, north of which rises Soufrière Volcano as a solitary cone (1,178 m) and the highest elevation on the island. The volcano erupted in 1902, killing 1,600 people. Later, a lava dome appeared in the summit crater in 1971 prior to the last eruption in 1979 (USGS, Cascades Volcano Observatory 2011). Towards the south, the land becomes progressively older and more mature, the valleys deeper and wider and ridges lower. Slopes are steep, particularly in the central backbone, and 50% of the island's total surface has slopes of 30 degrees or more, and only 20% have slopes less than 20 degrees (Barker 1981). Numerous lateral ridges are given off from the main axis. On the west, these are steep and sharp crested, separated by deep narrow gorges walled by lava cliffs. On the east, they slope more gradually with wider, flatter valleys opening in one or two places to coastal plains. In the central backbone, mountain slopes are too steep so cultivation has not been technically possible.

St. Vincent is composed entirely of volcanic ejecta (mainly pyroclastic) ranging in age from Pleistocene to Holocene. Soils have been studied and mapped by Watson et al. (1958) and the occurrence and distribu-

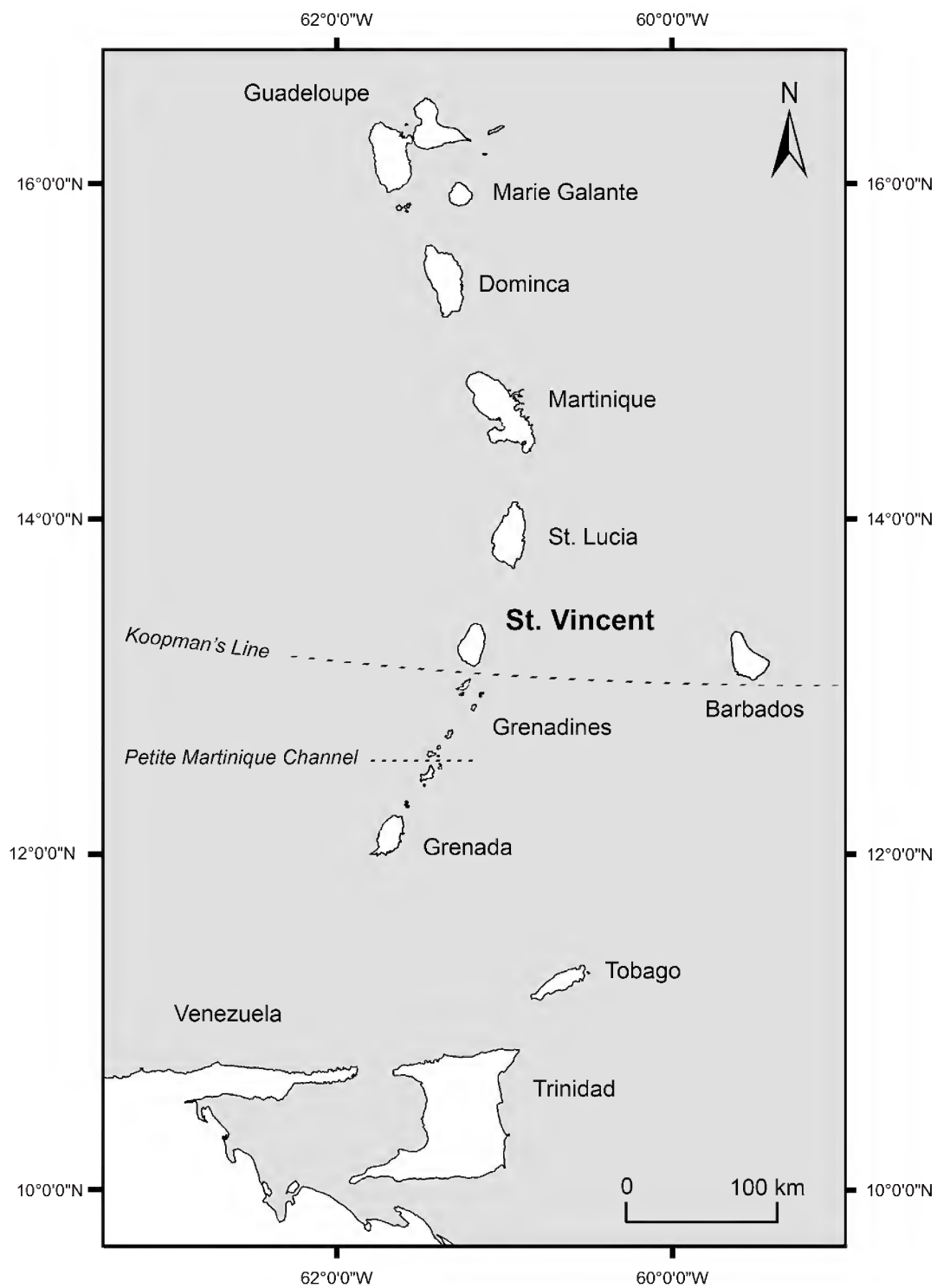


Figure 1. Map of the southern Lesser Antilles showing the position of the island of St. Vincent in relation to other islands in the region and northern South America.

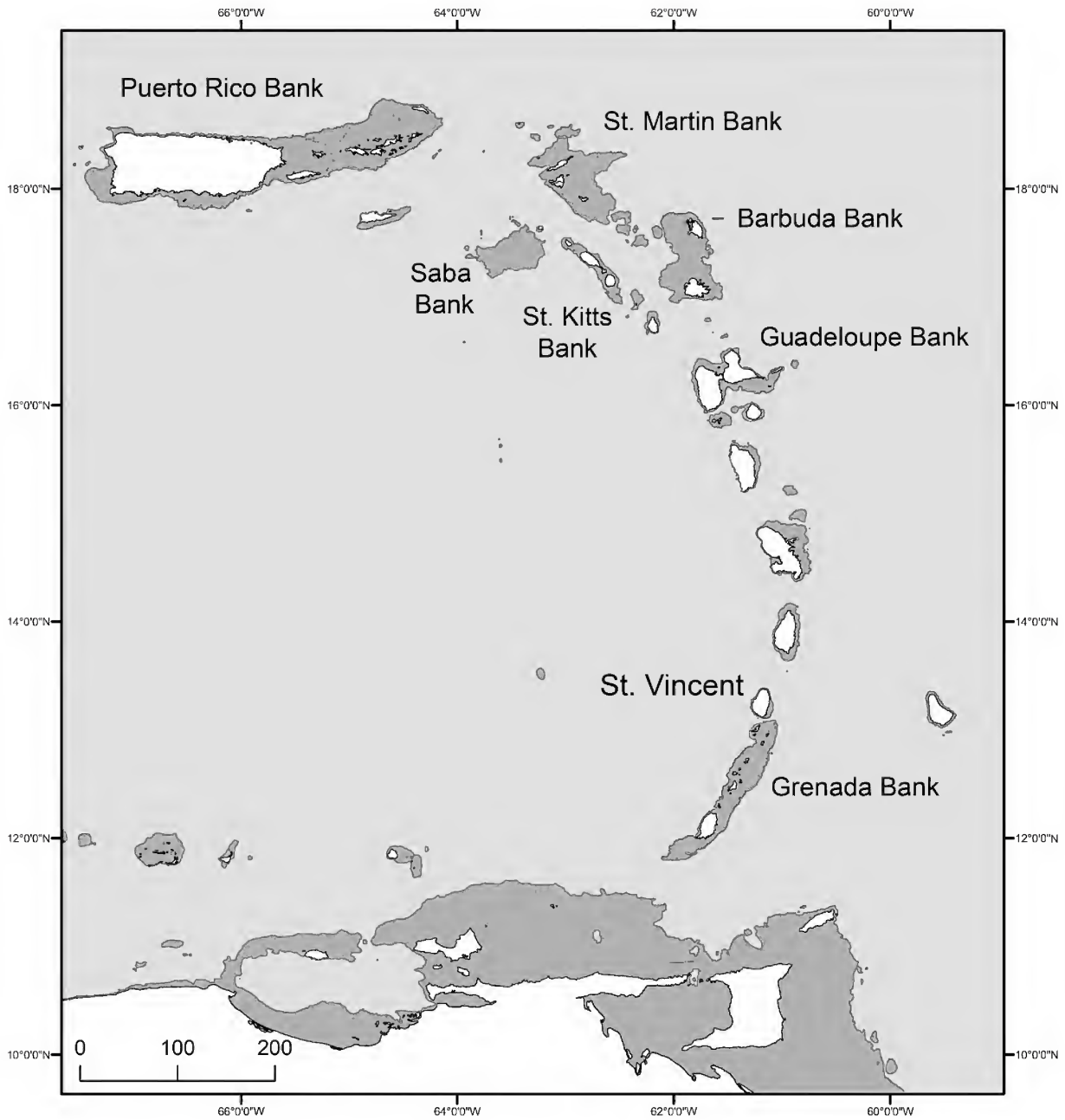


Figure 2. Bathymetric map of Puerto Rico and the Lesser Antilles. Dark grey shading represents potential extent of exposed land during the Pleistocene at last glacial maximum (26,500 to 19,000 years before present; sea levels ~130 m below current).

tion of natural vegetation types were summarized in Beard (1945, 1949; Birdsey et al. 1986). Rain forest is limited to small areas in the Colonarie, Cumberland, and Buccament valleys. Beard (1949) commented there were probably never many good stands of heavy forest because the slopes of the central mountains were too steep and loose to allow the forest to develop and where the slopes were gentler, the forest had been removed for agriculture. The term secondary rain forest was applied to a broad spectrum of forests disturbed by natural occurrences (for example, volcanic eruptions and hurricanes) or by human activities. Palm brake (see following section for scientific names of plant species discussed in text) covered large areas above 805 m. Sites of recent landslides are covered with thickets of small tree ferns or balisier, whereas older landslides were colonized by helecho gigante palm. On some uncultivated slopes near the coastlines, plant cover was a degraded dry scrub woodland, cactus scrub, and bush (Beard 1949). Small mangrove swamps composed of red, black, white, and buttonwood mangrove were part of southern St. Vincent (Caribbean Conservation Association 1991).

The ecosystems on the island have been shaped by hurricanes, volcanic activity, and earthquakes. The Soufriere Volcano at the northern end of St. Vincent last erupted in 1979, causing some evacuations and agriculture damage. Hurricane Allen, which was an h4 hurricane, passed between St. Vincent and St. Lucia on 4 August 1980, and Hurricane Tomas, which was a late season storm, passed over the northern end of the island on 31 October 2010. Damage resulted from flooding, storm surge, landslides, and winds. Because of its steep topography and loose pyroclastic soils, heavy rains during hurricanes led to significant landslides and slumping (Talbot 1983; Caribbean Hurricane Network 2014).

In 1979, St. Vincent and the Grenadines became an independent state within the British Commonwealth. Government reorganization in 1989 created the new Ministry of Health and the Environment in an attempt to refocus public attention on environmental concerns and coordinate the Government's environmental mission. In part, this allowed St. Vincent to exert the kind of environmental leadership, which once made it predominant, as the first eastern Caribbean island to establish both a botanical garden (1765) and a forest reserve (King's Hill in 1791).

Plant names.—The following are the common and scientific names of plants discussed in the text: agave (*Agave* sp.), Angeline (*Andira inermis*), Ashes Wood (*Miconia mirabilis*), Balata (*Manilkara bidentata*), balisier (*Heliconia* sp.), bamboo (Bambuseae), bananas (*Musa* sp.), Big Leaf Santinay (*Sloanea masoni*), Bitter Ash Tree (*Picrasma antillana*), Black Fig (*Ficus nymphaeifolia*), Black Mangrove (*Avicennia germinans*), Blue Mahoe (*Hibiscus elatus*), Breadfruit (*Artocarpus altilis*), Buttonwood Mangrove (*Conocarpus erectus*), Cabbage Bark (*Andira inermis*), Candlewood (*Dacryodes excelsa*), Caribbean Pine (*Pinus caribaea*), Caribbean Trumpet Fruit (*Tabebuia aurea*), Chaste Tree (*Vitex divaricata*), Cocoa (*Theobroma cacao*), Coconuts (*Cocos nucifera*), Crabwood (*Carapa guianensis*), Dasheen (*Colocasia esculenta*), Fiddlewood (*Citharexylum spinosum*), Galba (*Calophyllum calaba*), Genip (*Genipa americana*), Guava (*Psidium guajava*), Helecho Gigante (*Cyathea tenera*), Heliconias (*Heliconia psittacorum*), Jamaican Plum (*Spondias mombin*), Joint Bush (*Piper amalago*), Mango (*Mangifera indica*), Manjack (*Cordia sulcata*), Milktree (*Sapium caribaeum*), Nutmeg (*Myristica fragrans*), Oil Palm Tree (*Elaeis guineensis*), Palm Brake (*Prestoea montana*), Papaya (*Carica papaya*), pepper plant (*Piper* sp.), Red Mangrove (*Rhizophora mangle*), Rose Apple Tree (*Syzygium jambos*), Santinay (*Sloanea caribaea*), Soursop (*Annona muricata*), Spanish Ash (*Inga ingoides*), Teak (*Tectona grandis*), Tree Fern (*Cyathea arborea*), Trumpet Tree (*Cecropia peltata*), Waterwood (*Chimarrhis cymosa*), West Indian Locust (*Hymenaea courbaril*), White Cinnamon (*Nectandra membranacea*), Wild Mahoe (*Daphnopsis americana*), White Mangrove (*Laguncularia racemosa*), Wild Nutmeg (*Micropholis chrysophylloides*), Wild Plumrose (*Marlierea ferruginea*), and Wild Red Ginger (*Costus scaber*).

Mist-netting.—Field collection and sampling were accomplished primarily by mist-netting surveys, which consisted of 25 nights during two periods—24 July to 6 August 2005 (12 nights) and 23 May to 8 June 2006 (13 nights). Mist netting was conducted in a variety of habitats including naturally vegetated ravines or ghuts, access roads, trails, rivers, ponds, fruit plantations, botanical gardens, and other covered flyways. At each netting site, mist nets 2.8, 6, 9, 12, or 18 m in length by 2.8 m in height were set singly or in groups depending on local landscape features. Typically, five

to eight nets were set at 20 to 100 m intervals at each location to fill flyways as much as possible, opened near sunset, and monitored for three to five hours. Bats were placed in holding bags until the nets were closed. Bats were subsequently examined and measured—weight (g), length of forearm (mm), reproductive condition, tooth wear, presence of ectoparasites, scars, and any atypical physical attributes were recorded. We followed the methods of R. Larsen et al. (2007; see also Findley and Wilson 1983) for determining capture rates of bats (bats per net per night or BNN).

Roost surveys.— We also explored and collected specimen samples from six caves (Bat Cave, Cane Garden Point Cave, Chateaubelair Point Bat Hole, Dennis' Cave, Mt. Wynne Bat Caves, and Owia Big River Cave), two tunnels (Black Point Cave [Tunnel] and Grand Sable Tunnel), and three man-made structures (Arnos Vale Factory Ruins, Mount Pleasant Ruins, and Three River Ruins). These sites were visited during the daylight hours while the bats were in residence. Bats

were captured with gloved hands, hand nets, or mist nets erected in the larger caves and tunnels.

Museum voucher specimens.—During 2005–2006, our work on St. Vincent resulted in the collection of 677 voucher specimens of 12 species of bats subsequently deposited and examined in the research collections at the Museum of Texas Tech University (TTU). A survey of existing collection materials in natural history museums including the American Museum of Natural History (AMNH), National Museum of Natural History (NMNH), Carnegie Museum of Natural History (CM), University of Kansas (KU), Museum of Texas Tech University (TTU), Royal Ontario Museum (ROM), and University of Nebraska State Museum (UNSM) resulted in an additional 345 specimens available for study. Thus, we examined a total of 1,022 specimens for our analyses of the bats of St. Vincent. During our 25 nights of mist-netting work on St. Vincent, we captured and released an additional 1,291 bats.

SYSTEMATIC ACCOUNTS

The species accounts that follow are arranged in systematic order (Simmons 2005; Baker et al. 2016; Cirranello et al. 2016). The accounts include a list of specimens we examined and a list of additional records (a gazetteer of sites is provided in the Appendix). Distances were recorded in kilometers (km) or in miles (mi) as they appeared on original specimen labels. Similarly, elevations were reported in meters (m) or in feet (ft) as they appeared on original specimen labels. Weights were determined with a digital balance and recorded in grams (g). Embryo size was recorded as crown-rump length. Measurements were taken with digital calipers and recorded in millimeters. Cranial measurements were taken from museum vouchers and were taken following Hall (1946), except greatest length of skull in which we included the incisors. The length of the forearm is the distance from the olecranon process to the tip of the carpals with wing in the retracted position. Minitab 16 provided standard statistics for each sample set examined and paired t-tests were utilized to test for differences in group means.

Family Noctilionidae

Noctilio leporinus mastivus (Vahl, 1797)

Greater Fishing Bat

Specimens examined (32).—**Charlotte Parish:** Yambou River Gorge, W Peruvian Vale, 49 m [13°10'16.8"N, 61°09'14.8"W], 8 (TTU 105453–60). **St. Andrew Parish:** Lower Buccament River, Buccament, 2 m [13°11'30.2"N, 61°00'16.6"W], 12 (TTU 105744–55). **St. David Parish:** Bat Hole, 0.4 km N, 0.5 km W Chateaubelair, 2 m [13°17'40.2"N, 61°14'44.1"W], 8 (TTU 105816–23). **St. George Parish:** 1 km NE Brighton Village, 2 (UNSM 19278–79). **St. Patrick Parish:** Wallilabou, 10 m [13°14'54.2"N, 61°16'09.1"W], 1 (TTU 105987); Wallilabou Falls, 0.6 km E Wallilabou, 55 m [13°14'54.2"N, 61°15'37.7"W], 1 (TTU 105999).

Additional records.—**St. Patrick Parish:** G. M. Allen (1911) does not give a specific locality for the specimens that he reported from St. Vincent, but

examining the original Museum of Comparative Zoology catalog online indicates that they came from “Barrouallie”. **No Specific Parish:** no specific locality (Vaughan 1995; Vaughan and Hill 1996).

Specimens captured/released (36).—**St. Andrew Parish:** Lower Buccament River, Buccament, 36 m [$13^{\circ}11'30.2''\text{N}$, $61^{\circ}00'16.6''\text{W}$], 36.

This species represents a recent radiation within the genus *Noctilio*, having diverged from its sister species *N. albiventris* within the last million years (Pavan et al. 2013; Khan et al. 2014). Owing to the species' recent evolutionary history, studies focused on the intraspecific morphological and genetic variation of *N. leporinus* have resulted in conflicting taxonomic assessments. Davis (1973) identified three subspecies within *N. leporinus*—*N. l. leporinus* (distributed in South America east of the Andes Mountains, throughout Amazonia and the Guyana Shield), *N. l. mastivus* (distributed throughout Central America, the Caribbean, and in South America throughout Venezuela and along the western versant of the Andes Mountains into northern Ecuador), and *N. l. rufescens* (distributed in southern South America throughout Bolivia, Paraguay, northern Argentina and southern Brazil). However, genetic data presented in Pavan et al. (2013) and Khan et al. (2014) reveal two main lineages within *N. leporinus*, one corresponding to *N. l. mastivus* and the other to *N. l. leporinus*. To date, all specimens collected from within the range of *N. l. rufescens* are genetically indistinguishable from *N. l. leporinus* (Pavan et al. 2013; Kahn et al. 2014).

The available genetic data from *N. leporinus* provide evidence of dual invasions into the Caribbean by the species, with Central American populations colonizing the Greater Antilles and northern South American populations colonizing the southern Lesser Antilles (Lewis-Oritt et al. 2001; Genoways et al. 2010; Pavan et al. 2013; Kahn et al. 2014). Despite this observation, there was no clear genetic consensus regarding the most appropriate subspecific taxonomy for southern Lesser Antillean populations, including *N. leporinus* from St. Vincent. This was because a hybrid zone (situated in eastern Venezuela and the Guyana Shield) between populations identified as *N. l. mastivus* and *N. l. leporinus* likely existed in the regions from which southern Lesser Antillean populations presumably originated

(Genoways et al. 2010; Khan et al. 2014). Thus, additional studies are required to determine the extent of hybridization in mainland populations of *N. leporinus* and whether or not this hybrid zone has impacted the genetic makeup of southern Lesser Antillean populations. A strikingly similar pattern of dual Caribbean invasions and hybridization was found in the genus *Artibeus*, where *A. jamaicensis* (originating from Central America) and *A. planirostris* (originating from northern South America) have converged on St. Vincent (and surrounding islands) forming a hybrid zone in the southern Lesser Antilles (see *Artibeus schwartzi* species account below). With respect to Caribbean *N. leporinus*, future research must utilize advanced genetic techniques (for example, whole genome scans) to elucidate the evolutionary history of Greater Antillean and Lesser Antillean populations and to precisely identify zones of secondary contact between *N. l. mastivus* and *N. l. leporinus*. Until such data become available, we provisionally retain *N. l. mastivus* for the St. Vincent population (Fig. 3).

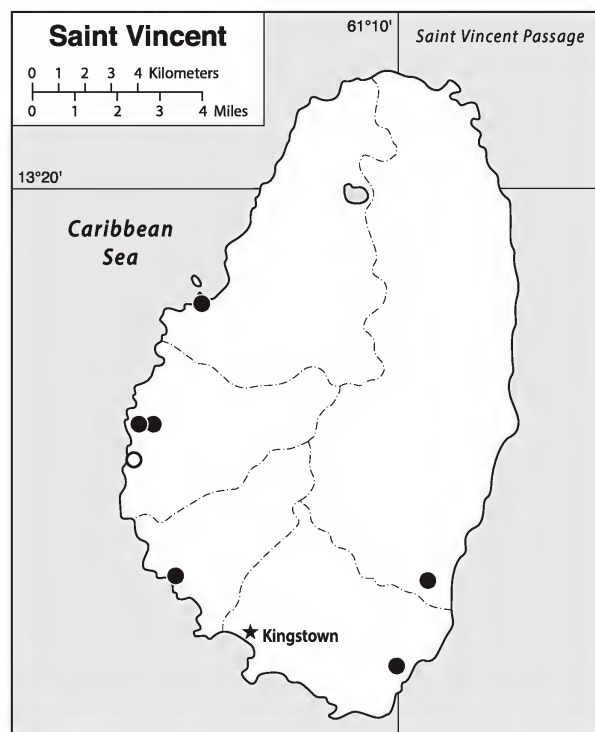


Figure 3. Map of the geographic distribution of *Noctilio leporinus* on the Lesser Antillean island of St. Vincent. Closed circles represent specimens examined and open circles represent literature records.

Table 1 presents length of forearm and seven cranial measurements for six male and four female *N. leporinus* from St. Vincent. Males averaged larger than females for all eight measurements. Although the average of male forearms was larger than those of females, they were not significantly different. All skull measurements were significantly larger in males when compared to female measurements at the $P \leq 0.05$ for three measurements (greatest length of skull, length of maxillary toothrow, and breadth across upper molars), at the $P \leq 0.01$ level for three measurements (zygomatic breadth, postorbital constriction, and mastoid breadth), and at the $P \leq 0.001$ for one measurement (condylobasal length). When comparing our measurements for females to those from Davis (1973), St. Vincent specimens fell within the ranges provided for the West Indies except condylobasal length and length of forearm, which were greater in length.

Noctilio leporinus, which has a widespread distribution in the Antilles (see Pedersen et al. 2013), was first reported from St. Vincent by G. M. Allen (1911) who noted specimens collected by Austin H. Clark in 1903. Clark reported to G. M. Allen (1911): “that this bat usually resorts by day to deep narrow clefts in the rocks, rather than to more open caves, and that its presence in such places may often be detected by its peculiar musky odor.” Clark obviously had experience with this species because he deposited 11 specimens of this species in the Museum of Comparative Zoology, Harvard University, all captured on 25 September 1903 at Barouallie. This species can be expected in coastal and lowland habitats anywhere there are large ponds, slow moving rivers, and wind-protected coastal areas where it can “fish” for food by use of its elongate hind limbs and toes. Although considered a piscivorous bat, *N. leporinus* consumes insects that make about the same percentage of its diet as small fishes, and less frequently consumes some crustaceans and arachnids (Brooke 1994).

We captured 68 *N. leporinus*, all in coastal or lowland habitats. One specimen was netted over a field (Wallilabou), not more than 50 m from the Wallilabou River. Presumably this juvenile (presence of metacarpal epiphyseal cartilage) was captured here as it was avoiding the vegetatively overgrown river, because of its novice flying skills. This area was heavily impacted by human activity with small garden plots. Trees in

the area included soursop, papaya, mango, trumpet tree, and wild plumrose. All *Noctilio* netted over water were presumably attempting to feed on small fish or invertebrates near the water surface or while commuting to foraging sites.

We netted 48 *N. leporinus* and observed many more along the Lower Buccament River (Fig. 4) on 24 May 2006. Two experienced bat biologists described the movement of two separate waves of these bats moving across the bay and into their mist net located on a sandbar in the mouth of the river. Each wave was well organized with bats flying in echelon formation, no more than one meter above the water’s surface. Behind the sand bar was a brackish pond about 100 by 20 m in size. Above the pond, the river passed through open agricultural fields with single or clusters of small trees, including mango, Spanish ash, genip, and fiddlewood. About 400 m south of the mouth of the river there was a series of nearly vertical seaside cliffs approximately 50 m tall that may have served as roosting sites for these bats. Mist nets also were placed above the upper end of the brackish pond and among some clusters of trees nearly 1 km upstream. Bat activity was focused on the pond, but as the evening progressed they dissipated with some individuals moving out around the cove, whereas others moved up the Buccament River toward higher elevations.



Figure 4. Photograph of the Lower Buccament River, St. Andrew Parish, St. Vincent. Photograph was taken about a kilometer from the river’s mouth. Forty-eight *Noctilio leporinus* were captured over the lower portion of the river on the night of 24 May 2006.

Table 1. Length of forearm and seven cranial measurements for 12 species of bats from the island of St. Vincent, Lesser Antilles. Significance levels comparing males and females appear in the row following the entry "Males."

Sex, catalog number, statistics, sample size	Length of forearm	Greatest length of skull	Condylolbasal length	Zygomatic breadth	Postorbital constriction	Mastoid breadth	Length of maxillary toothrow	Breadth across upper molars
<i>Noctilio leporinus mastivus</i>								
Males (N = 6)	ns	*	***	**	**	**	*	*
Mean $\pm$ SE	88.3 $\pm$ 0.69	27.1 $\pm$ 0.40	25.5 $\pm$ 0.14	20.0 $\pm$ 0.17	7.5 $\pm$ 0.06	18.9 $\pm$ 0.40	10.7 $\pm$ 0.07	12.9 $\pm$ 0.12
Range	(86.5–91.1)	(26.3–29.0)	(25.2–26.2)	(19.4–20.3)	(7.4–7.7)	(17.2–20.1)	(10.4–10.9)	(12.5–13.3)
Females (N = 4)								
Mean $\pm$ SE	86.9 $\pm$ 1.00	25.7 $\pm$ 0.12	24.4 $\pm$ 0.09	18.7 $\pm$ 0.22	7.0 $\pm$ 0.07	17.3 $\pm$ 0.10	10.3 $\pm$ 0.14	12.4 $\pm$ 0.14
Range	(84.1–88.7)	(25.4–26.0)	(24.2–24.6)	(18.1–19.1)	(6.9–7.3)	(17.0–17.5)	(9.9–10.5)	(12.2–12.7)
<i>Pteronotus fuscus</i>								
Males (N = 10)	ns	**	**	***	ns	**	**	ns
Mean $\pm$ SE	59.9 $\pm$ 0.25	22.1 $\pm$ 0.09	21.5 $\pm$ 0.07	12.6 $\pm$ 0.05	4.3 $\pm$ 0.04	11.6 $\pm$ 0.07	9.5 $\pm$ 0.04	8.2 $\pm$ 0.05
Range	(58.6–60.7)	(21.7–22.8)	(21.3–22.0)	(12.4–12.8)	(4.2–4.6)	(11.2–11.9)	(9.4–9.7)	(8.1–8.5)
Females (N = 10)								
Mean $\pm$ SE	59.3 $\pm$ 0.28	21.8 $\pm$ 0.06	21.2 $\pm$ 0.06	12.3 $\pm$ 0.04	4.3 $\pm$ 0.05	11.3 $\pm$ 0.06	9.4 $\pm$ 0.03	8.1 $\pm$ 0.07
Range	(58.0–60.3)	(21.5–22.1)	(20.9–21.5)	(12.2–12.5)	(4.1–4.7)	(10.9–11.7)	(9.1–9.5)	(7.6–8.5)
<i>Micronycteris buriri</i>								
Males								
N	16	12	11	12	12	12	12	12
Mean $\pm$ SE	38.4 $\pm$ 0.73	21.2 $\pm$ 0.34	18.8 $\pm$ 0.27	9.9 $\pm$ 0.16	4.4 $\pm$ 0.08	9.3 $\pm$ 0.14	8.2 $\pm$ 0.14	6.8 $\pm$ 0.16
Range	(36.4–39.5)	(20.7–21.8)	(18.3–19.2)	(9.6–10.2)	(4.3–4.6)	(9.1–9.5)	(7.9–8.4)	(6.6–7.2)
Female								
TTU 105773	39.2	21.7	19.3	10.1	4.6	9.4	8.2	7.3
TTU 105982	40.3	21.0	18.9	9.9	4.5	9.4	8.2	6.8

Table 1. (cont.)

Sex, catalog number, statistics, sample size	Length of forearm	Greatest length of skull	Condylolbasal length	Zygomatic breadth	Postorbital constriction	Mastoid breadth	Length of maxillary tooththrow	Breadth across upper molars
<i>Monophyllus plethodon plethodon</i>								
Males	ns	ns	ns	**	ns	*	ns	*
N	10	10	10	10	10	10	9	10
Mean ± SE	42.1 ± 0.25	23.1 ± 0.12	21.5 ± 0.11	10.1 ± 0.08	4.6 ± 0.04	9.9 ± 0.06	8.0 ± 0.06	5.8 ± 0.07
Range	(41.0–43.6)	(22.6–23.7)	(21.1–22.1)	(9.6–10.5)	(4.4–4.8)	(9.4–10.1)	(7.7–8.2)	(5.4–6.2)
Females								
N	11	12	12	12	12	12	12	12
Mean ± SE	41.8 ± 0.38	22.9 ± 0.13	21.4 ± 0.10	9.8 ± 0.06	4.7 ± 0.02	9.6 ± 0.07	8.0 ± 0.05	5.5 ± 0.05
Range	(39.6–43.5)	(22.2–23.6)	(21.1–22.1)	(9.5–10.1)	(4.6–4.8)	(9.2–10.1)	(7.8–8.4)	(5.2–5.9)
<i>Glossophaga longirostris rostrata</i>								
Males (N = 17)	ns	ns	ns	ns	ns	ns	ns	*
Mean ± SE	37.4 ± 0.19	22.5 ± 0.08	21.2 ± 0.07	9.8 ± 0.05	4.7 ± 0.03	9.4 ± 0.04	7.6 ± 0.05	5.8 ± 0.04
Range	(36.1–39.1)	(21.7–23.3)	(20.5–21.7)	(9.4–10.2)	(4.5–4.9)	(9.0–9.5)	(7.2–7.9)	(5.6–6.1)
Females (N = 19)								
Mean ± SE	37.1 ± 0.25	22.7 ± 0.06	21.3 ± 0.08	9.7 ± 0.04	4.7 ± 0.02	9.3 ± 0.03	7.7 ± 0.04	5.9 ± 0.03
Range	(33.6–38.5)	(22.2–23.1)	(20.5–22.0)	(9.5–10.1)	(4.6–4.9)	(9.2–9.5)	(7.3–8.0)	(5.6–6.2)
<i>Brachyphylla cavernarum cavernarum</i>								
Males	ns	ns	ns	ns	ns	ns	ns	ns
N	24	27	27	25	27	25	25	27
Mean ± SE	65.0 ± 0.25	31.5 ± 0.22	28.7 ± 0.15	17.2 ± 0.13	6.5 ± 0.03	14.8 ± 0.08	11.2 ± 0.07	11.6 ± 0.06
Range	(62.1–68.4)	(28.4–32.8)	(25.7–30.0)	(14.7–17.7)	(6.1–6.7)	(13.6–15.3)	(10.8–12.1)	(10.6–12.2)
Females								
N	20	22	22	22	22	22	22	22
Mean ± SE	65.5 ± 0.47	31.7 ± 0.14	28.8 ± 0.11	17.3 ± 0.10	6.5 ± 0.04	14.8 ± 0.08	11.3 ± 0.04	11.7 ± 0.06
Range	(60.8–69.8)	(30.7–33.0)	(27.7–29.5)	(16.3–17.9)	(6.3–7.2)	(13.6–15.3)	(11.0–11.6)	(11.2–12.1)

Table 1. (cont.)

Sex, catalog number, statistics, sample size	Length of forearm	Greatest length of skull	Condylolbasal length	Zygomatic breadth	Postorbital constriction	Mastoid breadth	Length of maxillary tooththrow	Breadth across upper molars
<i>Sturnira pailsoni paulsoni</i>								
Males	ns	**	**	**	ns	ns	*	**
N	14	15	15	14	15	15	14	14
Mean $\pm$ SE	43.1 $\pm$ 0.21	23.1 $\pm$ 0.09	20.9 $\pm$ 0.08	13.2 $\pm$ 0.07	5.9 $\pm$ 0.04	11.6 $\pm$ 0.05	6.8 $\pm$ 0.03	8.1 $\pm$ 0.03
Range	(42.2–44.4)	(22.5–23.8)	(20.5–21.5)	(12.7–13.6)	(5.7–6.1)	(11.3–12.0)	(6.5–7.0)	(7.8–8.2)
Females								
N	14	15	15	14	15	15	14	14
Mean $\pm$ SE	42.8 $\pm$ 0.25	22.3 $\pm$ 0.11	20.2 $\pm$ 0.12	12.8 $\pm$ 0.13	5.9 $\pm$ 0.04	11.4 $\pm$ 0.06	6.6 $\pm$ 0.05	7.8 $\pm$ 0.05
Range	(41.5–44.3)	(21.7–23.0)	(19.2–20.7)	(11.5–13.3)	(5.7–6.2)	(10.8–11.6)	(6.3–7.0)	(7.3–8.0)
<i>Artibeus lituratus palmarum</i>								
Males								
TTU 105292	72.1	32.2	28.2	19.5	6.7	17.4	11.5	14.1
KU 110181	—	30.3	27.1	19.8	7.0	16.4	11.2	14.1
<i>Artibeus schwartzi</i>								
Males	ns	ns	ns	ns	ns	ns	ns	ns
N	17	21	21	21	21	21	21	21
Mean $\pm$ SE	64.1 $\pm$ 0.44	30.7 $\pm$ 0.16	27.4 $\pm$ 0.13	19.2 $\pm$ 0.14	7.3 $\pm$ 0.04	16.3 $\pm$ 0.10	11.2 $\pm$ 0.06	14.1 $\pm$ 0.10
Range	(60.5–67.4)	(28.5–31.6)	(25.9–28.5)	(17.8–20.6)	(7.0–7.7)	(15.1–17.0)	(10.6–11.7)	(12.9–14.8)
Females								
N	25	31	31	31	31	31	31	31
Mean $\pm$ SE	64.7 $\pm$ 0.59	30.6 $\pm$ 0.14	27.4 $\pm$ 0.13	19.1 $\pm$ 0.15	7.4 $\pm$ 0.03	16.0 $\pm$ 0.09	11.1 $\pm$ 0.07	14.0 $\pm$ 0.09
Range	(59.8–69.3)	(28.7–31.7)	(25.7–28.3)	(17.4–20.2)	(6.9–7.7)	(14.5–16.9)	(10.1–11.7)	(12.9–14.8)

Table 1. (cont.)

Sex, catalog number, statistics, sample size	Length of forearm	Greatest length of skull	Condylabasal length	Zygomatic breadth	Postorbital constriction	Mastoid breadth	Length of maxillary tooththrow	Breadth across upper molars
<i>Ardops nichollsi vincentensis</i>								
Males	**	***	***	***	*	***	***	***
N	11	13	12	12	13	13	13	13
Mean ± SE	41.2 ± 0.30	20.5 ± 0.90	18.2 ± 0.13	13.1 ± 0.12	5.6 ± 0.05	10.8 ± 0.07	6.3 ± 0.05	8.5 ± 0.06
Range	(40.0–43.2)	(20.0–21.1)	(17.5–19.3)	(12.2–13.5)	(5.3–6.0)	(10.3–11.2)	(6.1–6.6)	(8.3–8.9)
Females								
N	12	12	11	12	12	12	12	12
Mean ± SE	43.2 ± 0.50	21.6 ± 0.11	19.0 ± 0.11	13.7 ± 0.08	5.8 ± 0.07	11.4 ± 0.05	6.8 ± 0.05	9.1 ± 0.04
Range	(40.0–45.7)	(21.0–22.2)	(18.3–19.5)	(13.3–14.1)	(5.4–6.2)	(11.2–11.7)	(6.6–7.1)	(8.9–9.3)
<i>Molossus molossus molossus</i>								
Males (N = 19)	***	***	***	**	*	***	**	*
Mean ± SE	38.3 ± 0.20	16.5 ± 0.13	15.1 ± 0.11	10.2 ± 0.08	3.5 ± 0.03	9.8 ± 0.07	5.8 ± 0.05	7.5 ± 0.06
Range	(36.8–39.8)	(15.5–17.6)	(13.9–16.0)	(9.4–10.7)	(3.4–3.8)	(9.0–10.3)	(5.3–6.1)	(6.9–7.9)
Females (N = 18)								
Mean ± SE	37.3 ± 0.12	15.9 ± 0.08	14.5 ± 0.06	9.9 ± 0.04	3.4 ± 0.03	9.4 ± 0.04	5.5 ± 0.04	7.3 ± 0.04
Range	(36.5–38.3)	(15.3–16.6)	(14.0–15.1)	(9.5–10.2)	(3.3–3.6)	(9.0–9.7)	(5.2–5.9)	(7.0–7.5)
<i>Tadarida brasiliensis antillarum</i>								
Males (N = 5)	ns	ns	ns	ns	ns	ns	ns	ns
Mean ± SE	37.5 ± 0.55	15.7 ± 0.22	14.7 ± 0.04	9.5 ± 0.23	3.6 ± 0.05	8.9 ± 0.19	5.6 ± 0.02	6.9 ± 0.23
Range	(35.5–38.5)	(15.4–16.6)	(14.6–14.8)	(9.2–10.4)	(3.4–3.7)	(8.7–9.7)	(5.5–5.7)	(6.5–7.8)
Females (N = 7)								
Mean ± SE	38.2 ± 0.22	15.8 ± 0.12	14.8 ± 0.10	9.5 ± 0.09	3.7 ± 0.05	9.0 ± 0.13	5.6 ± 0.03	6.8 ± 0.11
Range	(37.6–38.9)	(15.3–16.3)	(14.3–15.0)	(9.2–9.9)	(3.4–3.8)	(8.6–9.5)	(5.5–5.7)	(6.6–7.4)

We netted eight of these bats in the Yambou River Gorge, which was not a typical “gorge,” being an inclined bank of 1.5 to 2 m from the river to the fruit plantation service road. This was an agricultural, flood plain landscape, not more than 1.5 km from the Atlantic coast and mouth of the river. The river at the net site was riparian, but open and wide enough to accommodate two nets in the river, five across the service road (north of river), and an 18-m mist net between two mango trees on the south side of the river. Other flora in the general area included bananas, palms, and members of the genus *Piper*. The river gorge where we set nets was in the rising portion of coastal flood plain, with swift flowing water, ripples, and many rocks in the riverbed. One of our nets was set across the river underneath a large buttressed tree that we surmised to be a *Noctilio* roost because the air was permeated with characteristic *Noctilio* odors.

At a place 1 km NE Brighton Village, two *N. leporinus* were captured in a mist net placed over the Diamond River. This area was probably more impacted by human activity than any other place that we worked on the island—it was located on the western edge of the former Diamond Airfield, which at one time served as the island’s main airport. The surrounding area had developed as an industrial park, which was at various stages of disrepair and abandonment with the relocation of the airport. The river was in reality a small stream that was only about a meter wide at most points, with steep muddy banks. Two nets were set in an area where a dirt track crossed the river, creating a pool of water that was about four to five meters wide. There were only a few stunted trees along the riverbank, otherwise grass was the primary ground cover. Other species captured here included *G. longirostris* (9), *A. schwartzi* (3), and *M. molossus* (1).

We identified a day roost for this species at Bat Hole on Chateaubelair Point. The vertical crevice was about 7 m tall and could only be accessed via boat. The upper reaches of the crevice were stained brown from bat droppings. From the boat, we used hand nets to reach 3 to 4 m up into the crevice to urge the bats into our bags. In this manner, we were able to collect eight specimens.

Four female *N. leporinus* taken on 26 May 2006 in the Yambou River Gorge were lactating and one was

carrying a single embryo that measured 45 in crown-rump length. Three of four females captured on 2 August 2005 at Chateaubelair Point cave were lactating. Of the 20 females netted at Lower Buccament on 5 August 2005, 11 were lactating. A female taken along the Wallilabou River on 6 August 2005 was a volant juvenile. Although these reproductive data were from only a narrow slice of time, they seem to fit well with the reproductive cycle for the species as summarized by Hood and Jones (1984). Based on information in the literature, they believed that breeding for the species begins in November and December, with gestation in the winter and spring, and births occurring between late April and June. The females from St. Vincent had given birth by late May, although one individual was still carrying a near term fetus. About half of the females were still lactating in early August, with some of the juveniles becoming independent and flying on their own. An adult male obtained on 24 May had testes that were in a scrotal position and measured 5.5 in length, whereas two non-scrotal males taken on the same date had testes lengths of 4.0 and 6.0. In early August, four scrotal males had testes lengths of 7.0, 7.5, 7.5, and 7.5, whereas six males with testes in an inguinal position had an average testes length of 4.7 (3.0–5.5).

Three lactating females taken in late May weighed 54.7, 51.9, and 51.6, whereas the female carrying the large fetus weighed 64.4. The mean weight of nine lactating female taken in early August was 51.1 (47.4–55.4), whereas seven females evincing no reproductive activity taken at this time had a mean weight of 49.4 (44.2–53.4). A male taken in late May and considered to have testes in a scrotal position weighed 69.1, whereas a non-scrotal male taken at this time weighed 53.0. Seven adult males taken on 5 August weighed on average 66.6 (61.1–75.6).

Family Mormoopidae

Pteronotus fuscus (J. A. Allen, 1911)

Brown Mustached Bat

Specimens examined (44).—**Charlotte Parish:** Colonarie River, 1 km S, 2.4 km W South Rivers, 248 m [13°14'10.4"N, 61°09'52.7"W], 3 (TTU 105650–52); La Soufriere Trail, 0.7 km N, 5.1 km W Orange Hill, 646 m [13°19'22.8"N, 61°10'01.2"W], 1 (TTU 105360); La Soufriere Trailhead, 3.7 km W Orange Hill, 420 m [13°19'00.2"N, 61°09'01.2"W], 2 (TTU

105379–80); Owia Big River Cave, 0.3 km S, 0.3 km W Owia, 97 m [13°22'15.1"N, 61°08'56.1"W], 21 (TTU 105400–07, 105707–19); Above Owia, 0.5 km S, 0.3 km W Owia, 172 m [13°22'10.7"N, 61°08'57.1"W], 1 (TTU 105388); Perseverance, 0.2 km N, 3.1 km W Georgetown, 250 m [13°16'38.7"N, 61°08'52.0"W], 3 (TTU 105421–23). **St. Andrew Parish:** Lower Buccament River, Buccament, 2 m [13°11'30.2"N, 61°00'16.6"W], 1 (TTU 105756); Parrot Lookout, Vermont Nature Trail, 2.3 km N, 1.75 km E Vermont, 496 m [13°13'20.2"N, 61°12'43.4"W], 3 (TTU 105804–06). **St. David Parish:** Morgan Woods, 0.4 km N, 2.4 km E Richmond, 253 m [13°18'28.9"N, 61°12'27.9"W], 4 (TTU 105538–41); 0.7 km S, 1.75 km E Rose Hall, 379 m [13°15'46.9"N, 61°13'35.4"W], 1 (TTU 105501). **St. Patrick Parish:** Convent, 0.4 km N, 3 km E Grove, 440 m [13°14'53.5"N, 61°12'32.1"W], 1 (TTU 105976); Wallilabou Falls, 0.6 km E Wallilabou, 55 m [13°14'54.2"N, 61°15'37.7"W], 1 (TTU 105558); Wallilabou River Gorge, 0.1 km S, 1.8 km E Wallilabou, 170 m [13°14'31.7"N, 61°15'8.0"W], 2 (TTU 105575–76).

Additional records.—**St. Andrew Parish:** rain forest at Vermont [13°12'N, 61°13'W] (Vaughan 1995; Vaughan and Hill 1996). **St. Patrick Parish:** rain forest at Cumberland Valley, ≈ Cumberland [≈13°15'N, 61°15'W] (Vaughan 1995; Vaughan and Hill, 1996).

Specimens captured/released (3).—**Charlotte Parish:** Owia Big River Cave, 0.3 km S, 0.3 km W Owia, 97 m [13°22'15.1"N, 61°08'56.1"W], 3.

Specimens of *Pteronotus* were first reported from St. Vincent by Vaughan and Hill (1996) under the name *P. parnellii* based on five adults from the rain forests of Vermont and Cumberland Valley. During our work on the island, we collected an additional 44 individuals of *Pteronotus* from 13 separate locations (Fig. 5). The taxonomy of the *Pteronotus parnellii* complex (Smith 1972) is currently in flux and it is likely that a number of species are cryptic and represent unnamed taxa. Although Dávalos (2006) applied the name *Pteronotus rubiginosus* to populations in northern South America, recent molecular and phonic data from the Guianan Shield provide clear evidence of unrecognized species diversity (Clare et al. 2013; Thoisy et al. 2014; López-Wilchis et al. 2016; Pavan and Marroig 2016,

2017). In particular, Pavan and Marroig (2016, 2017) performed a robust morphometric and phylogenetic analyses of *Pteronotus* collected across the Neotropical distribution of the genus, including 20 specimens collected from St. Vincent. Their results support the hypothesis of unrecognized species diversity across northern South America, and suggest that the appropriate binomial for the St. Vincent *Pteronotus* is *P. fuscus*. This classification was based on statistical support in both mitochondrial and nuclear gene datasets uniting specimens collected from northern Venezuela, Trinidad and Tobago, and St. Vincent. In light of the molecular results of Pavan and Marroig (2016, 2017) we provisionally recognize the St. Vincent population of *Pteronotus* as *P. fuscus*.

On the mainland of South America, Gutiérrez and Molinari (2008) plotted the distribution of *P. fuscus* in Venezuela as occurring north of the Cordillera de la Costa, a branch of the Andes, and westward around Lake Maracaibo, possibly into Colombia. The north

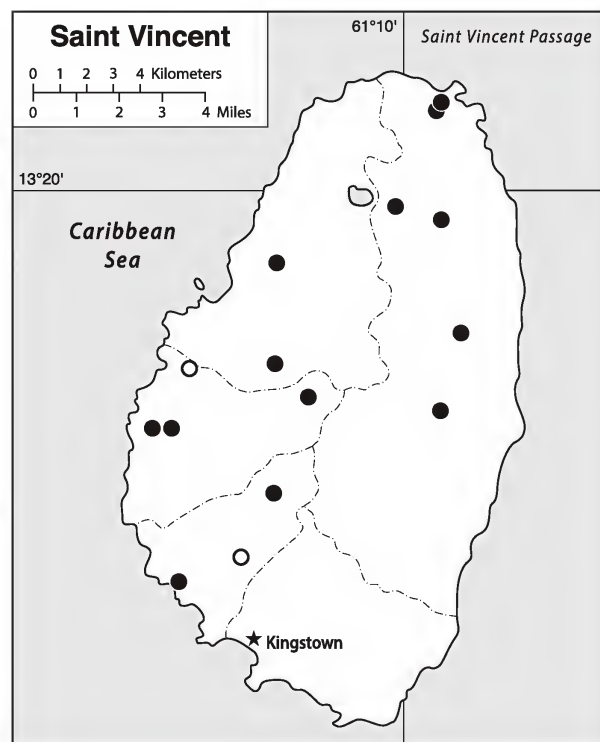


Figure 5. Map of the geographic distribution of *Pteronotus fuscus* on the Lesser Antillean island of St. Vincent. Closed circles represent specimens examined and open circles represent literature records.

coast and Lake Maracaibo area of Venezuela are very dry, with the coastal areas being narrow, especially to the east where it may be only a few kilometers wide. However, given the potential for cryptic diversity, we recommend additional studies that include genetic analyses of samples *P. fuscus*, especially those collected from near the type locality (Las Quiguas, 5 mi south of Puerto Cabello, 650 ft., Carabobo, Venezuela; J. A. Allen 1911). According to the collector of the holotype M. A. Carriker, Jr., Las Quiguas lies in the San Esteban valley which: “opens upon the sea near Puerto Cabello, and extends southeastward, flanked on either side by high ridges, and rising rapidly in its upper part to the crest of the coast range. The pass at its head has an altitude of 4443 feet [1,355 m], while the range rises on either side to about 6000 feet [1,830 m] at the highest points” (J. A. Allen 1911). The phylogenetic relationship of *P. fuscus* from St. Vincent with respect to specimens from Guyana and Trinidad suggests a colonization of St. Vincent from northern South America. Pavan and Marroig (2017) place the divergence of *P. fuscus* and *P. mesoamericanus/mexicanus* at about 1.3 million years ago in the mid-Pleistocene; therefore, entrance of *P. fuscus* into the Lesser Antilles would be subsequent to that date.

Table 1 provides measurements for samples of 10 male and 10 female *Pteronotus fuscus* from St. Vincent. Male length of forearms was longer, but not significantly, than female forearms. Males averaged larger than females in five of seven cranial measurements, in which males were significantly larger ($P \leq 0.01$) than females for condylobasal length, mastoid breadth, and length of maxillary tooththrow and ($P \leq .001$) zygomatic breadth, but the difference was not significant for post-orbital constriction and breadth across upper molars. Table 2 presents a comparison of four selected measurements of the St. Vincent population with populations of *P. fuscus* from Trinidad and Venezuela, *P. parnellii* from Jamaica, and *P. portoricensis* from Puerto Rico, all of which are members of the subgenus *Phyllodia*. Clearly, individuals in the St. Vincent population are morphologically larger in all four measurements than either of the two species from islands in the Greater Antilles. On the other hand, the St. Vincent material appears to fit closely with the populations of *P. fuscus* from Trinidad and Venezuela. The population of *P. fuscus* from Trinidad has a length of forearm that av-

eraged longer than any other population, being more than 61 mm, whereas the other four samples averaged 60 mm or less. However, in the three cranial measurements the St. Vincent and Trinidad populations group together, averaging larger than the three samples from Venezuela. In condylobasal length the Trinidad-St. Vincent samples averaged 21.2 or more, whereas the Venezuelan populations averaged 20.7 or less. Similar comparisons for zygomatic breadth are 12.3 or greater as opposed to 12.3 or less and for length of maxillary tooththrow are 9.4 or greater as opposed to 9.3 or less. More morphometric data and analyses will be necessary before we can fully understand the geographic variation in this recently recognized species. The phylogenetic relationship of *P. fuscus* from St. Vincent with respect to specimens from Guyana and Trinidad suggests the most logical route for *P. fuscus* populations to have arrived on St. Vincent was from the south on Trinidad, Guyana, or the north coast of the mainland in Venezuela.

During our work on St. Vincent, we netted 47 individuals in a variety of habitats and located one cave day roost (Owia Big River Cave). Our nets captured this species at 11 sites ranging from sea level (mouth of Buccament River) to 646 m (La Soufriere Trail). We captured *Pteronotus fuscus* in nets set across trails (Parrot Lookout, Vermont Trail; Convent; La Soufriere Trailhead; and Rose Hall) and in nets set across streams/ rivers (Colonaire River; Buccament River; Wallilabou River Falls; and Wallilabou River Gorge). This species was caught in association with *N. leporinus*, *M. buriri*, *B. cavernarum*, *G. longirostris*, *M. plethodon*, *A. nichollsi*, *A. schwartzi*, *S. paulsoni*, *M. molossus*, and *T. brasiliensis*.

Owia Big River Cave was the single day roost for *Pteronotus fuscus* that we discovered on St. Vincent. The cave was situated adjacent to a pool of water approximately 10 m long and 7 m wide and no more than 3 m deep in the channel of Owia Big River. Half of the pool was open to the sky and the other half was under an overhanging rock ledge. The river flowed from west to east but this pool was created in part by debris and rocks at its east end. The majority of bats were located in two alcoves at the eastern end of the cave, where the rocky floor was covered with guano. The cave at this point extended approximately 5 m deeper into the cliff face with a height of about 1.3 m. The

Table 2. Length of forearm and three cranial measurements for three species of the genus *Pteronotus* (subgenus *Phyllodia*).

Sex, statistics, sample size	Length of forearm	Condylobasal length	Zygomatic breadth	Length of maxillary toothrow
<i>Pteronotus parnellii</i> —Jamaica (Genoways et al. 2005)				
Males (N = 10)				
Mean $\pm$ SE	53.2 $\pm$ 0.30	19.2 $\pm$ 0.04	11.3 $\pm$ 0.04	8.9 $\pm$ 0.03
Range	(52.0-55.2)	(19.1-19.5)	(11.0-11.5)	(8.7- 9.0)
Females (N = 10)				
Mean $\pm$ SE	53.4 $\pm$ 0.25	18.9 $\pm$ 0.07	11.0 $\pm$ 0.04	8.7 $\pm$ 0.04
Range	(52.6-55.1)	(18.4-19.1)	(10.9-11.2)	(8.5- 8.9)
<i>Pteronotus portoricensis</i> —Puerto Rico (Gannon et al. 2005)				
Males (N = 17)				
Mean $\pm$ SE		19.1 $\pm$ 0.17	11.0 $\pm$ 0.16	7.0 $\pm$ 0.10
Range		(18.8-19.4)	(10.7-11.4)	(6.9-7.2)
Females (N = 13)				
Mean $\pm$ SE		18.9 $\pm$ 0.15	10.9 $\pm$ 0.16	7.0 $\pm$ 0.16
Range		(18.7-19.2)	(10.6-11.2)	(6.9-7.2)
<i>Pteronotus fuscus</i> —St. Vincent (This study)				
Males (N = 10)				
Mean $\pm$ SE	59.9 $\pm$ 0.25	21.5 $\pm$ 0.07	12.6 $\pm$ 0.05	9.5 $\pm$ 0.04
Range	(58.6-60.7)	(21.3-22.0)	(12.4-12.8)	(9.4-9.7)
Females (N 10)				
Mean $\pm$ SE	59.3 $\pm$ 0.28	21.2 $\pm$ 0.06	12.3 $\pm$ 0.04	9.4 $\pm$ 0.03
Range	(58.0-60.3)	(20.9-21.5)	(12.2-12.5)	(9.1-9.5)
<i>Pteronotus fuscus</i> —Trinidad (Smith 1972)				
Males-females (N=15)				
Mean $\pm$ 2 SE	61.3 $\pm$ 1.90	21.3 $\pm$ 0.14	13.0 $\pm$ 0.13	9.6 $\pm$ 0.06
Range	(58.4-64.3)	(20.9-21.7)	(12.6-13.3)	(9.5-9.9)
<i>Pteronotus fuscus</i> —vicinity of San Esteban, Carabobo, Venezuela (Smith 1972)				
Males-females (N=19)				
Mean $\pm$ 2 SE	59.9 $\pm$ 0.67	20.3 $\pm$ 0.18	12.3 $\pm$ 0.12	9.2 $\pm$ 0.06
Range	(57.5-61.4)	(19.0-20.8)	(12.0-12.6)	(8.9-9.5)
<i>Pteronotus fuscus</i> —Isla de Margarita, Nueva Esparta, Venezuela (Smith 1972)				
Males-females (N=15)				
Mean $\pm$ 2 SE	58.0 $\pm$ 0.52	20.3 $\pm$ 0.13	12.1 $\pm$ 0.13	9.2 $\pm$ 0.08
Range	(56.3-60.0)	(19.8-20.6)	(11.7-12.6)	(9.0-9.4)

Table 2. (cont.)

Sex, statistics, sample size	Length of forearm	Condylbasal length	Zygomatic breadth	Length of maxillary toothrow
<i>Pteronotus fuscus</i> —northern Venezuela (Gutiérrez and Molinari 2008)				
Males (N)	65	61	61	62
Mean $\pm$ SD	59.3 $\pm$ 1.6	20.7 $\pm$ 0.3	12.3 $\pm$ 0.03	9.3 $\pm$ 0.2
Range	(55.0-62.6)	(19.9-21.8)	(11.1-12.9)	(8.8-9.5)
Females (N)	45	44	42	44
Mean $\pm$ SD	60.0 $\pm$ 1.5	20.5 $\pm$ 0.3	12.3 $\pm$ 0.03	9.2 $\pm$ 0.2
Range	(57.7-63.2)	(19.9-21.2)	(11.7-12.9)	(8.5-9.5)

second alcove of the cave extended at a right angle to the first to a depth of approximately 12 m with a height of about 3.5 m. Both alcoves housed individuals of *Pteronotus fuscus* and *B. cavernarum*, but roosting in separate areas and not intermingled. The locality Above Owia was approximately 200 m up stream from Big River Cave. Nets were placed along the river and in the riparian forest.

One specimen of *P. fuscus* was taken along the La Soufriere Trail—the highest elevation (646 m) from which we obtained this species on St. Vincent. As we travelled up this flank of the volcano, the vegetation shifted from tropical forest to tree fern forest to elfin woodland. The rim of the volcano (1,234 m) was above the tree line and exposed to high winds. This particular net site was located below the rim, along the trail where the secondary forest created a closed canopy over the trail.

We took four specimens at Morgan Woods (253 m), which were the most individuals of this species that we netted in a foraging area on a single night. Four nets (two 12 m, one 18 m, one 9 m) were set along the forested road we used to reach the site. One 18-m net was placed across a parking lot at the site. In the open areas around the parking lot were tall stands of plants of the genus *Piper*.

Three individuals of *P. fuscus* were netted in two foraging areas at Perseverance (250 m). Two nets were placed across a large water treatment reservoir—“Perseverance Sanitation Plant.” This concrete struc-

ture consisted of three conjoined tanks that were easily accessed by bats. The reservoir was surrounded by mowed grass and one pepper plant. Four additional nets were set on a road below the reservoir, a walking path, and across the small river. The predominant habitat in this area was secondary lowland tropical forest. In addition to *P. fuscus*, other species captured at this site were *G. longirostris*, *M. plethodon*, *A. schwartzi*, *S. paulsoni*, and *M. molossus*.

Of the 14 female bats captured between 27 May and 5 June 2006, 11 were carrying single embryos, whereas the other three evinced no gross reproductive activity. The average crown-rump length of these embryos was 27.7 (25–30). The tight clustering of the sizes of these fetuses would indicate a highly synchronous breeding season. Of the 11 adult females obtained between 27 July and 5 August 2005, five were lactating, whereas the other six appeared to be not reproductively active. Although these reproductive data represent a very narrow segment of time, they match the reproductive cycle (Wilson 1973; Herd 1983) reported for *P. parnellii*, which is now viewed as a taxonomically distinct species restricted to the populations on some of the islands in the Greater Antilles (Dávalos 2006). Wilson (1973) believed that this species followed a reproductive cycle of “seasonal monestry,” with the young born at the end of the dry season. Breeding occurs in January, parturition in May and early June, and lactation can occur until the end of July. Even though the population of *P. fuscus* on St. Vincent is the only Lesser Antillean population of this species, it appears to be following a seasonal monoestry pattern very closely.

At the end of May and in early June, four scrotal males had testes lengths that averaged 4.25 (3.5–5.5), whereas seven males with testes in an inguinal position from this time period had testes that averaged 3.3 (2.5–4.0). Four males with testes in a scrotal position taken in a later time period (late July and early August) had testes lengths that averaged the same as the males from May–June, 4.25 (3.0–5.0). However, four males with testes in an inguinal position from this latter time had testes lengths that averaged smaller than the comparable males from May–June, 2.6 (2.0–3.0).

Mean weight of 11 pregnant females caught between 27 May and 5 June on St. Vincent was 19.4 (18.3–21.0), whereas three non-reproductive females taken during this time had weights of 13.7, 15.2, and 15.7. The average weight of 12 males from the end of May and early June was 17.2 (15.2–20.1). Five lactating females taken in late July had a mean weight of 16.1 (15.5–16.8), which was very close to the mean weight of six non-reproductive females taken in late July and early August, 16.2 (15.3–17.1). The average weight of 10 males from this latter time period was 17.0 (14.8–18.7), which was similar to the weights recorded for males at the end of the dry season in May–June.

Family Phyllostomidae

Micronycteris buriri P. Larsen, Siles, Pedersen,
and Kwiecinski, 2011

St. Vincent Big-eared Bat

Specimens examined (19).—**Charlotte Parish:** Colonarie River, 1 km S, 2.4 km W South Rivers, 248 m [13°14'10.4"N, 61°09'52.7"W], 4 (TTU105640–43); La Soufriere Trail, 0.7 km N, 5.1 km W Orange Hill, 646 m [13°19'22.8"N, 61°10'01.2"W], 4 (TTU 105352–55). **St. Andrew Parish:** Parrot Lookout, Vermont Nature Trail, 2.3 km N, 1.75 km E Vermont, 496 m [13°13'20.2"N, 61°12'43.4"W], 2 (TTU 105773–74); Waterworks, 1.25 km N, 1.6 km E Vermont, 310 m [13°12'35.6"N, 61°12'52.0"W], 1 (TTU 105473). **St. David Parish:** Morgan Woods, 0.4 km N, 2.4 km E Richmond, 253 m [13°18'28.9"N, 61°12'27.9"W], 1 (TTU 105535); 0.75 km S, 2.3 km E Rose Hall, 377 m [13°15'51.2"N, 61°13'25.7"W], 2 (TTU 105507–08). **St. George Parish:** Mt. St. Andrew, 1.75 km N, 0.3 km E Green Hill, 633 m [13°11'17.9"N, 61°12'56.8"W], 1 (TTU 105548). **St. Patrick Parish:** Convent, 0.4 km N,

3 km E Grove, 440 m [13°14'53.5"N, 61°12'32.1"W], 2 (TTU 105971–72); Mount Wynne Cave, Mount Wynne Bay, 0 m [13°13'03.6"N, 61°16'30.4"W], 2 (TTU 105981–82).

Additional records (Vaughan 1995; Vaughan and Hill 1996).—**St. Andrew Parish:** forest and plantation at Vermont [≈13°12'N, 61°13'W]. **St. Patrick Parish:** Wallilabou River valley [≈13°14'54"N, 61°15'38"W]; sea caves at Mount Wynne beach [13°13'03.6"N, 61°16'30.4"W]. **St. George Parish:** Dennis' Cave, Cane Garden [13°08'16.9"N, 61°13'36.0"W].

Big-eared bats of the genus *Micronycteris* Gray 1866 are a common component of Neotropical bat fauna and occur in South America, Central America, Mexico, and in the southern Caribbean as far north as Grenada. This recently described species was first reported from St. Vincent as *Micronycteris megalotis* by Vaughan and Hill (1996) based on five adult specimens (four males, one female) taken in forests and plantations at Vermont and Wallilabou valleys and in sea caves at Mount Wynne beach and Dennis' Cave in Cane Garden. The Little Big-eared Bat, *Micronycteris megalotis*, was historically considered to be the commonest and widely distributed species in the genus (Alonso-Mejía and Medellín 1991; Vaughan and Hill 1996; Porter et al. 2007; Williams and Genoways 2008); however, the historically defined species actually represents a complex of several unrecognized taxa (P. Larsen et al. 2011; Siles et al. 2013).

Morphological and molecular data indicated that the St. Vincent population of *Micronycteris* represents a distinct species separate from *M. megalotis* and was subsequently named *M. buriri* (P. Larsen et al. 2011). *Micronycteris buriri*, known only from St. Vincent, was distinguished from its closest relative, *M. megalotis* from Trinidad and Tobago, by its larger size (Table 1) and distinct craniodental features, including non-bilobed upper incisors, hypsodont lower incisors, very prominent cingula in upper and lower incisors, and very shallow basisphenoid pits separated by a poorly developed septum only in the posterior region (P. Larsen et al. 2011). The genetic data reported in P. Larsen et al. (2011) showed a sister relationship between *M. buriri* and *M. megalotis* from Tobago, and the authors hypothesized that *M. buriri* likely evolved in isolation

on St. Vincent during the Pleistocene. Because only a single adult female specimen of *M. megalotis* has been reported from Grenada (NMNH 267684), Genoways et al. (1998) questioned the authenticity of this report in light of extensive bat surveys of the island, but accepted the record because of the St. Vincent population. The single measurement reported for this female *M. megalotis* (length of forearm, 34.2) was clearly within the range of those reported for specimens collected from Trinidad and Tobago (see P. Larsen et al. 2011). The two measured female from St. Vincent (Table 1) had forearm lengths of 39.2 and 40.3 and the range for males was 36.4 to 39.5; thus, the Grenada specimen has a shorter forearm than any of the St. Vincent material. With respect to the *M. megalotis* complex, there are at least four lineages identified by P. Larsen et al. (2011) that require taxonomic clarification.

In 2005 and 2006 we collected nineteen specimens of *M. buriri* from nine sites (Fig. 6) located from sea level to 646 m elevation, primarily in forested areas, but two individuals were taken from the Mt. Wynne sea cave. The St. Vincent Big-eared Bat was always captured in association with *A. schwartzi* (singly with *A. schwartzi* at Mount Wynne cave). We captured *M. buriri* within Mount Wynne Cave, situated along Mount Wynne Bay on the west coast of the island. The cave was located at the north end of a black sand beach under a bluff undercut by the surf. The bluff was covered with dry tropical thorn forest with a profusion of agave. The entrance to the cave was at surf level with an opening of approximately 3 m high and 4 m wide. The cave was not deep, approximately 10 to 15 m, and high enough for an adult human to stand. There were only a few bats present and tidal surge had erased any evidence of multiple species use or permanence of the cave (Fig. 7).

Dennis' Cave in Cane Garden was another day roost where this new species of bat was captured by Vaughan and Hill (1996). Members of our field team visited this cave in 2006 but only obtained specimens of *A. schwartzi*. The cave appeared to have been created by surf action on a cliff face composed of an agglomeration of remixed pyroclastic elements. Large pyroclastic cobbles and some driftwood were piled at the cave entrance. Bats were roosting in holes in ceiling left by cobble when it eroded and fell to the floor.

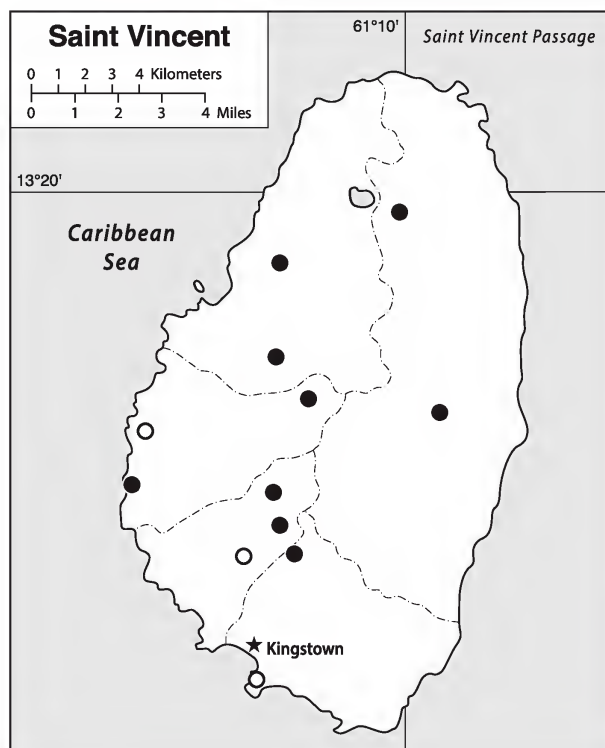


Figure 6. Map of the geographic distribution of *Micronycteris buriri* on the Lesser Antillean island of St. Vincent. Closed circles represent specimens examined and open circles represent literature records.



Figure 7. Photograph of the entrance to Mt. Wynne Cave, St. Patrick Parish, St. Vincent. Two individuals of *Micronycteris buriri* were captured inside of this sea cave.

We captured four St. Vincent Big-eared Bats apparently foraging along the Colonaire River at Morris Pasture. In some areas of the upper Colonaire River were stands of primary rain forest, with extensive areas of secondary rain forest covering the mountains on both sides of the river, but some of the area around our collecting site was a managed blue mahoe forest. With the varied topography and habitats in the area of our work, there were many species of trees that are of value to bats including helecho gigante, candlewood, pepper plant, wild red ginger, big leaf santinay, white cinnamon, angelina, West Indian locust, ashes wood, trumpet tree, waterwood, wild nutmeg, fiddlewood, and teak. Mist nets were placed in the pasture, along the edge of the pasture and into the edge of the forest, along forest trails, and along the river and a waterfall. Two nets were placed across the road bounded by joint bush and three were set end-to-end (28 m) across the forest to the river. One big-eared bat was taken in the top river net, two were obtained in nets set across the trail in the middle of the field, and the fourth was netted at the edge of the forest bordering Morris Pasture. Species collected alongside *M. buriri* in these nets were: *Pteronotus*, *Glossophaga*, *A. schwartzi*, *Ardops*, *Sturnira*, and *Molossus*.

Unfortunately, our data provide little insight into the reproductive cycle of this newly described species of bat. Only three females were captured during our work—one on 1 August and two on 6 August—and none presented with any observable reproductive activity. Sixteen males were captured between 27 May to 4 June and 28 July to 3 August, with all being judged to be in a non-reproductive state having the testes in an inguinal position. The only hint of active reproduction in these bats was a male taken on 3 August 2005 in which the phalangeal epiphyses were not completely closed. This was the smallest of our male specimens with a length of forearm of 36.4. The testes length of seven males captured at the end of May and early June averaged 2.4 (1.5–3.5), whereas three males taken at the end of July and early August had testes lengths of 2.0, 2.0, and 3.0.

The three females taken during our studies weighed 8.1, 8.1, and 8.6. Nine males taken in late May and early June weighed on average 7.9 (7.4–8.6), as did five males taken in late July and early August, 7.9 (7.4–8.4).

Monophyllus plethodon plethodon Miller, 1900
Insular Single-leaf Bat

Specimens examined (63).—**Charlotte Parish:** 1.2 km N, 2 km W Greiggs, 445 m [13°13'18.2"N, 61°10'42.7"W], 2 (TTU 105312–13); 3.2 km N, 2.2 km W Mesopotamia, 2 (CM 83169–70); Golden Grove, 1.5 km N, 2.7 km W Mesopotamia, 410 m [13°13'58.3"N, 61°11'32.7"W], 2 (TTU 105336–37); La Soufriere Trail, 0.7 km N, 5.1 km W Orange Hill, 648 m [13°19'22.8"N, 61°10'01.2"W], 4 (TTU 105356–59); La Soufriere Trailhead, 3.7 km W Orange Hill, 420 m [13°19'00.2"N, 61°09'01.2"W], 2 (TTU 105377–78); Perseverance, 0.2 km N, 3.1 km W Georgetown, 250 m [13°16'38.7"N, 61°08'52.0"W], 2 (TTU 105419–20); Montreal trap, 1.5 km N, 1.5 km W Richland Park, 473 m [13°12'30.7"N, 61°11'20.4"W], 5 (TTU 105671–75). **St. Andrew Parish:** Mt. St. Andrew, 0.35 km S, 3.0 km E Pembroke, 501 m [13°11'12.6"N, 61°13'07.0"W], 1 (TTU 105487); Parrot Lookout, Vermont Nature Trail, 2.3 km N, 1.75 km E Vermont, 496 m [13°13'20.2"N, 61°12'43.4"W], 29 (TTU 105775–803); Vermont Nature Trail, 1.6 mi E Vermont (by road), 4 (NMNH 580663, 580692–94). **St. David Parish:** Morgan Woods, 0.4 km N, 2.4 km E Richmond, 253 m [13°18'28.9"N, 61°12'27.9"W], 2 (TTU 105536–37); 0.3 km S, 2.2 km E Rose Hall, 435 m [13°15'58.3"N, 61°13'21.9"W], 2 (TTU 105491–92); 0.75 km S, 2.3 km E Rose Hall, 377 m [13°15'51.2"N, 61°13'25.7"W], 2 (TTU 105509–10). **St. George Parish:** Clifton Hill, 400 ft, 1 (KU 110088); 0.6 km S Mesopotamia, 1 (CM 83171). **St. Patrick Parish:** Convent, 0.4 km N, 3 km E Grove, 440 m [13°14'53.5"N, 61°12'32.1"W], 2 (TTU 105509–10).

Additional records.—**St. George Parish:** Presbytère de Kingston (Breuil 1997). **No Specific Parish:** no specific locality (Breuil and Masson 1991; Vaughan 1995; Vaughan and Hill 1996).

Specimens captured/released (19).—**Charlotte Parish:** Golden Grove, 1.5 km N, 2.7 km W Mesopotamia, 410 m [13°13'58.3"N, 61°11'32.7"W], 11; La Soufriere Trail, 0.7 km N, 5.1 km W Orange Hill, 646 m [13°19'22.8"N, 61°10'01.2"W], 1; La Soufriere Trailhead, 3.7 km W Orange Hill, 420 m [13°19'00.2"N, 61°09'01.2"W], 5. **St. Andrew Parish:** Parrot Lookout, Vermont Nature Trail, 2.3 km N, 1.75

km E Vermont, 496 m [13°13'20.2"N, 61°12'43.4"W], 1. **St. David Parish:** 0.75 km S, 2.3 km E Rose Hall, 377 m [13°15'51.2"N, 61°13'25.7"W], 1.

This nectarivorous/pollenivorous species was found to be widely distributed on St. Vincent (Fig. 8), but nowhere was it the most abundant species. Schwartz and Jones (1967) reviewed the genus *Monophyllus*, reducing recognized species from six to two (*M. redmani* and *M. plethodon*). They recognized a single species in the Lesser Antilles (*M. plethodon*), with the nominate subspecies restricted to Barbados, the remainder of the Lesser Antilles were represented by the subspecies *M. p. luciae* and a fossil subspecies, *M. p. frater*, from Puerto Rico.

Genoways et al. (2011) compared the morphometrics of Insular Single-leaf Bat populations from Barbados (type locality for *M. p. plethodon*) and St. Lucia (type locality for *M. p. luciae*) to study the rela-

tionship between these two named taxa in the southern Lesser Antilles. They found that the “validity of *M. p. luciae* must be seriously questioned” because the male bats from Barbados were significantly different from males on St. Lucia in five of eight measurements, whereas the females were significantly different in only two measurements. Because the location of St. Vincent forms an equilateral triangle with these two islands, we took the opportunity to further investigate the relationship between these taxa (Table 3). Females from St. Vincent grouped with females from St. Lucia in two measurements (length of forearm and length of maxillary tooththrow) in which significant differences were found between St. Lucia and Barbados populations, averaging 0.01 mm larger than St. Lucia bats in length of forearm and the same in length of maxillary tooththrow. In the non-significant measurements, the St. Vincent females averaged within 0.2 mm or less of the other two populations in them all. The results for males gave a slightly clearer picture for the five significantly different measurements. For postorbital constriction and length of maxillary tooththrow, the mean for the St. Vincent population was the same as the value for the St. Lucia population. For the other three measurements (greatest length of skull, zygomatic breadth, and mastoid breadth) for which the values for the Barbados and St. Lucia populations were significantly different, the mean values for the St. Vincent population fell between the means of the other two samples. Finally, for the non-significant measurement, the population from St. Vincent averaged larger than Barbados and St. Lucia for length of forearm and breadth across upper molar and had the same mean value as the Barbados population for condylobasal length.

When Schwartz and Jones (1967) studied *Monophyllus*, they stated: “It is purely on the basis of the holotype that we recognize *M. p. plethodon* as distinct from other Lesser Antillean populations.” The holotype of *M. p. plethodon* was smaller than other specimens of *Monophyllus plethodon*, including the second specimen from Barbados. Schwartz and Jones (1967) were uncertain about their decision in recognizing both *M. p. plethodon* and *M. p. luciae* and opined that additional material from these islands could alter their decision. It is now clear that members of the population of *Monophyllus plethodon* from Barbados were not smaller than those on St. Lucia and in the case of males they were in fact significantly larger. The addition of material from

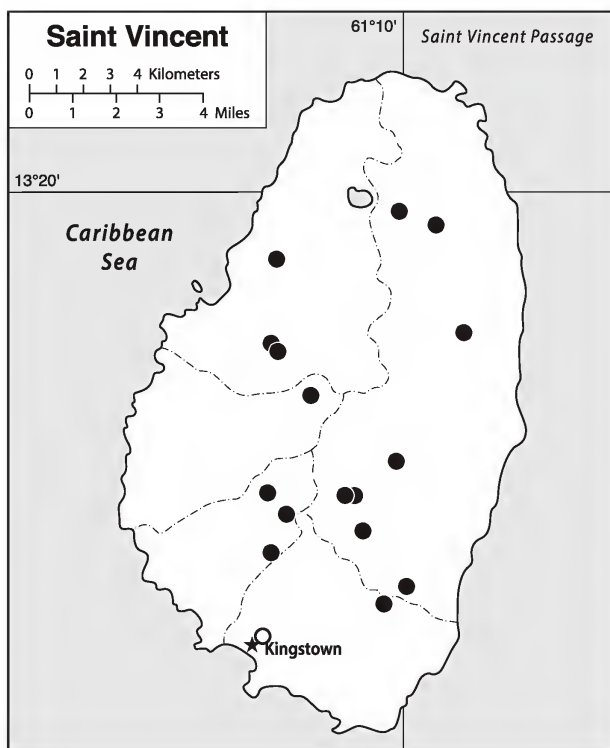


Figure 8. Map of the geographic distribution of *Monophyllus plethodon* on the Lesser Antillean island of St. Vincent. Closed circles represent specimens examined and open circles represent literature records.

Table 3. Comparisons of the morphological size of male and female *Monophyllus plethodon* from the Lesser Antillean islands of Barbados, St. Vincent, and St. Lucia. Measurements for samples from St. Lucia are from Pedersen et al. (2018).

Measurements	Males			Females		
	Barbados (N=9)	St. Vincent (N=10)	St. Lucia (N=14)	Barbados (N=10)	St. Vincent (N=12)	St. Lucia (N=15)
Length of forearm	41.8±0.28	42.1 ± 0.25	41.7±0.17	40.5±0.21	41.8 ± 0.38	41.7±0.23
Greatest length of skull	23.3±0.07	23.1 ± 0.12	22.9±0.09	23.1±0.09	22.9 ± 0.13	23.1±0.11
Condylobasal length	21.5±0.08	21.5 ± 0.11	21.4±0.11	21.5±0.05	21.4 ± 0.10	21.5±0.11
Zygomatic breadth	10.3±0.05	10.1 ± 0.08	10.0±0.08	9.7±0.13	9.8 ± 0.06	9.8±0.07
Postorbital constriction	4.8±0.06	4.6 ± 0.04	4.6±0.03	4.8±0.04	4.7 ± 0.02	4.7±0.04
Mastoid breadth	10.1±0.04	9.9 ± 0.06	9.8±0.05	9.7±0.05	9.6 ± 0.07	9.7±0.05
Length of maxillary toothrow	7.8±0.04	8.0 ± 0.06	8.0±0.05	7.8±0.05	8.0 ± 0.05	8.0±0.06
Breadth across upper molars	5.6±0.08	5.8 ± 0.07	5.7±0.07	5.5±0.06	5.5 ± 0.05	5.5±0.04

St. Vincent further clouded this situation. There was some tendency for the St. Vincent material to fall with the St. Lucia material as shown by two measurements for males and two for females. However, for three measurements the St. Vincent material was intermediate between the values from the other two islands appearing to be intergrades between them. In other measurements there were no significant differences among the three samples. It is now our opinion that there is no continuing need to recognize the taxon *Monophyllus plethodon luciae* Miller 1902 and it should be placed as a junior synonym of *Monophyllus plethodon plethodon* Miller 1900. Therefore, *Monophyllus plethodon plethodon* is a Lesser Antilles endemic, being distributed from Anguilla (Genoways et al. 2007c) southward to St. Vincent and Barbados, having been collected on all major islands (Pedersen et al. 2013). This leaves the fossil subspecies *M. p. frater* from Puerto Rico as the only other taxonomically recognized population within the species. Clearly, contemporary morphometric and molecular analyses of these bats from throughout their geographic range would be useful in confirming these results and elucidating the evolutionary history of the species.

Table 1 provides the length of forearm and seven cranial measurements for 10 males and 12 females from

St. Vincent. Length of forearm measurements (Table 1) for females and males fall within ranges of samples examined by Homan and Jones (1975) with male forearms averaging larger than female. Males were larger than females for six of seven cranial measurements, with the average for female postorbital constriction slightly greater than the male average. Statistically significant secondary sexual variation was found for larger male zygomatic breadth ($P \leq 0.01$), mastoid breadth ($P \leq 0.05$), and breadth across the upper molars ($P \leq 0.05$).

Vaughan Jennings et al. (2004) found the echolocation calls of *M. plethodon* from St. Vincent were frequency modulated, of very low intensity, and contained at least three harmonics, with the most energy in the second harmonic. They also found that these bats had wings with average aspect ratios and wing tip shape, and high wing loading. Vaughan Jennings et al. (2004) concluded that this combination of characters allowed the *M. plethodon* to not only fly slowly in cluttered space while foraging on pollen and small fruits but also to achieve fast commuting flight in open space.

Three insular single-leaf bats were captured in four mist nets set along a road and under a mango tree at the lowest elevation studied (377 m) at Rose Hall. There were several types of other fruits available in the

area, including Jamaican plum, rose apple, bananas, guava, breadfruit, pepper plant, and Caribbean trumpet fruit. We also collected *M. buriri*, *G. longirostris*, *A. schwartzi*, and *S. paulsoni* at this site. We captured two individuals along the ridge northwest of Greiggs at an elevation of 445 m. The vegetation in this foraging area was dominated by banana plantations surrounded by remnant patches of native plants, such as pepper plant and helecho gigantes, whose flowers should attract these pollenivores (Fig. 9).

We collected bats at Convent, which was located in the headwaters of the Cumberland River, near the Hermitage Forestry Station. There were areas of primary rain forest in the upper reaches of the Cumberland River, but there was considerable evidence of human activity in the area of the station, including an old sugar mill, a sawmill, and a managed forest with an access road ending near a logged area of cabbage barks. The Forestry Department acquired some of these lands in the 1960's and then instituted reforestation with Caribbean pine and blue mahoe. There were a number of guava trees scattered through the area and two fig trees were noted near the open area. Other important trees in the area included pepper plant, candlewood, big leaf santinay, angeline, West Indian locust, ashes wood, waterwood, balata, helecho gigante, and wild mahoe. At this location, we set 12 nets along the access road, near and across a tributary of the Cumberland River, uphill from the Forestry Station, near the sawmill, and the grassy opening in the pine plantation. Only two *M. plethodon* were captured—one in a net across the stream and the other in the open grassy area. Six other species of bats were captured on this evening before a major rain storm hit at 2200 hr—*P. fuscus*, 1; *M. buriri*, 2; *G. longirostris*, 5; *A. schwartzi*, 19; *S. paulsoni*, 23; and *M. molossus*, 1.

Montreal trap near Richland Park was part of a catchment system to maintain water quality and quantity for the Mesopotamian Valley and the Yambou River system. The site at 473 m was located near the agreed upon point where secondary rain forests and forest plantations lie above the farming areas of the Mesopotamian Valley below. The forest at the upper edge of the site included such important trees as big leaf santinay, black fig, helecho gigante, and wild mahoe. A major portion of this field site was a Caribbean pine plantation, but



Figure 9. Photograph of the field site northwest of Greiggs, Charlotte Parish, St. Vincent. Much of the tropical forest has been removed from this area and replaced with agricultural fields and gardens. Two *Monophyllus plethodon* were captured at this site at an elevation of 445 meters.

also many native plants were flowering during our visit in early August. We placed 17 nets among the pines, in a small patch of bananas, along and across the road and stream, in a clearing near the water tank, and adjacent to a cultivated field of dasheen. Individuals of *M. molossus* were observed flying at 1850 hr and the first net captures were *A. schwartzi* and *G. longirostris* at 1910 hr. Five *M. plethodon* were netted—two over the streambed, one in a short net across the road near the pines, one in a net in the pines, and one in the banana grove. Five other species were obtained here including *B. cavernarum* (1), *G. longirostris* (12), *A. nicholli* (1), *A. schwartzi* (49), and *S. paulsoni* (30).

Twenty-one female *M. plethodon* were captured between the end of May and early June during the transition from dry to wet seasons on St. Vincent. Ten of these females were lactating, eight evinced no gross reproductive activity, and three were post-lactating. Thirteen males taken during this time period had testes in a scrotal position of which five had a mean length of testes of 2.7 (2.0–3.0) and six had testes in an inguinal position among which three had a testes length of 2.0, 3.0, and 3.5. Ten females were captured at the end of July and early August at the height of the wet season. Eight of these females were lactating and two revealed no reproductive activity. Twenty-seven males were

captured during this period, with four of the scrotal males having a mean testes length of 3.5 (3.0–4.0), whereas 12 males having testes in an inguinal position averaged shorter testes lengths, 2.8 (2.0–3.5). A female captured on 22 August 1967 was lactating. There are only scattered reports of reproduction in *M. plethodon*, but Genoways et al. (2005) found the reproductive cycle of the closely related species, *M. redmani*, on Jamaica, to most closely fit the monestry pattern, with gestation beginning in December, parturition occurring from March into May, and lactation from March until July. Reproductive information for the St. Vincent population of *M. plethodon* was limited to 25 May–22 August where only lactating and non-reproductive females were taken; however, these data do not disagree with a monoestrous pattern.

Ten lactating females collected between late May and early June had a mean weight of 12.7 (10.9–14.1), whereas three post-lactating individuals weighed 12.4, 12.4, and 13.2, and seven non-reproductive females had a mean weight of 13.1 (12.4–14.4). Nine scrotal males weighed on average 15.3 (14.0–16.8), whereas six non-scrotal males averaged 13.8 (9.8–16.0). During late July and early August, five lactating females had a mean weight of 12.8 (11.9–13.9), whereas two non-reproductive females weighed 11.9 and 12.1. During this period four males with testes in a scrotal position had a mean weight of 13.2 (12.6–13.9), whereas 12 males with testes in an inguinal position weighed on average 13.5 (12.1–15.1).

***Glossophaga longirostris rostrata* Miller, 1898**

Miller's Long-tongued Bat

Specimens examined (217).—**Charlotte Parish:** Argyle, 1 (AMNH 207998); Byera Hill, Black Point Tunnel, 5 m [13°15'46.0"N, 61°07'01.0"W], 13 (TTU 105615–27); Colonarie River, 1 km S, 2.4 km W South Rivers, 248 m [13°14'10.4"N, 61°09'52.7"W], 3 (TTU 105637–39); Fancy River trap, 0.6 km S, 0.3 km E Fancy, 150 m [13°22'31.7"N, 61°08'56.1"W], 3 (TTU 105658–60); Golden Grove, 1.5 km N, 2.7 km W Mesopotamia, 410 m [13°13'58.3"N, 61°11'32.7"W], 3 (TTU 105332–34); Tunnel, 0.5 km N, 0.9 km W Grand Sable, 100 m [13°16'18.3"N, 61°07'42.6"W], 8 (TTU 105349, 105424–30); 1.2 km N, 2 km W Greiggs, 445 m [13°13'18.2"N, 61°10'42.7"W], 2 (TTU 105310–11);

La Soufriere Trail, 0.7 km N, 5.1 km W Orange Hill, 646 m [13°19'22.8"N, 61°10'01.2"W], 4 (TTU 105340–41, 105350–51); La Soufriere Trailhead, 3.7 km W Orange Hill, 420 m [13°19'00.2"N, 61°09'01.2"W], 2 (TTU 105374–75); 3.2 km N, 2.2 km W Mesopotamia, 6 (CM 83119–24); Mesopotamia, 350 ft., 2 (KU 110046–47); Montreal trap, 1.5 km N, 1.5 km W Richland Park, 473 m [13°12'30.7"N, 61°11'20.4"W], 2 (TTU 105670, 105690); 0.35 km N, 0.2 km W Old Sandy Bay, 57 m [13°21'41.4"N, 61°08'07.9"W], 2 (TTU 105296–97); Above Owia, 0.5 km S, 0.3 km W Owia, 172 m [13°22'10.7"N, 61°08'57.1"W], 2 (TTU 105386–87); Perseverance, 0.2 km N, 3.1 km W Georgetown, 250 m [13°16'38.7"N, 61°08'52.0"W], 2 (TTU 105415–16); 1 km S Peruvian Vale, 15 (CM 83125–39); Yambou River Gorge, W Peruvian Vale, 49 m [13°10'16.8"N, 61°09'14.8"W], 4 (TTU 105447–50). **St. Andrew Parish:** Lower Buccament River, Buccament, 2 m [13°11'30.2"N, 61°00'16.6"W], 2 (TTU 105740–41); Mt. St. Andrew, 0.35 km S, 3.0 km E Pembroke, 501 m [13°11'12.6"N, 61°13'07.0"W], 1 (TTU 109115); Parrot Lookout, Vermont Nature Trail, 2.3 km N, 1.75 km E Vermont, 496 m [13°13'20.2"N, 61°12'43.4"W], 2 (TTU 105771–72); Petroglyph site, Pembroke, ca. 1 mi. W Cane Grove, 2 (NMNH 580661–62); Trailhead for Vermont Nature Trail, 1.4 km N, 1.5 km E Vermont, 310 m [13°12'18.8"N, 61°12'53.4"W], 2 (TTU 105810–11); Vermont Nature Trail, 1.6 mi E Vermont (by road), 14 (NMNH 580678–91); Waterworks, 1.25 km N, 1.6 km E Vermont, 310 m [13°12'35.6"N, 61°12'52.0"W], 2 (TTU 105471–72). **St. David Parish:** Falls of Baleine, 13 km S, 2.6 km W Fancy, 130 m [13°22'13.6"N, 61°11'36.2"W], 1 (TTU 105522); Morgan Woods, 0.4 km N, 2.4 km E Richmond, 253 m [13°18'28.9"N, 61°12'27.9"W], 2 (TTU 105533–34); 0.3 km S, 2.2 km E Rose Hall, 435 m [13°15'58.3"N, 61°13'21.9"W], 1 (TTU 105490); 0.7 km S, 1.75 km E Rose Hall, 379 m [13°15'46.9"N, 61°13'35.4"W], 2 (TTU 105499–500); 0.75 km S, 2.3 km E Rose Hall, 377 m [13°15'51.2"N, 61°13'25.7"W], 1 (TTU 105506). **St. George Parish:** Arnos Vale Factory Ruin, 18 m [13°08'47.8"N, 61°12'42.7"W], 2 (TTU 105824–25); Botanical Garden, Liberty Lodge, 71 m [13°09'55.5"N, 61°13'40.8"W], 6 (TTU 105864–66, 105906–08); Brighton, 2 (AMNH 207999–800); 1 km NE Brighton Village, 9 (UNSM 19268–76); 1.3 km N, 2.7 km E Calliagua, 17 (CM 83140–56); Calliagua, 7 (AMNH 219140–46); Clifton Hill, 400 ft., 15 (KU 110048–52, 110056–65);

Dennis' Cave, Cane Garden, 2 m [13°08'16.9"N, 61°13'36.0"W], 2 (TTU 105916–17); Evesham, 155 m [13°10'10.7"N, 61°10'12.9"W], 2 (TTU 105924–25); E side Kings Hill, 1 (NMNH 580658); Kingstown, 3 (1 KU 110072; 2 ROM 79029–30); 0.6 km S Mesopotamia, 12 (CM 83157–68); Milikin Bay, near Prospect, 10 m [13°07'59.3"N, 61°10'03.5"W], 4 (TTU 105944–45, 105956–57); Mount Pleasant Ruin, 104 m [13°09'02.9"N, 61°09'13.1"W], 4 (TTU 105938–41); Mt. St. Andrew, 1.75 km N, 0.3 km E Green Hill, 633 m [13°11'17.9"N, 61°12'56.8"W], 2 (TTU 105546–47); Ratho Mill, 1 (KU 150924); Richmond Hill, 3 (ROM 60162–63, 74417); Rose Cottage area, Villa Point, West Side, between Indian Bay and Greathead Bay, 2 (NMNH 580056–57); 0.5 mi SW Stubbs, 200 ft., 5 (KU 110067–71). **St. Patrick Parish:** Convent, 0.4 km N, 3 km E Grove, 440 m [13°14'53.5"N, 61°12'32.1"W], 2 (TTU 105969–70); Lower Bellwood, 2 (KU 150934–35); Wallilabou, 10 m [13°14'54.2"N, 61°16'09.1"W], 2 (TTU 105985–86); Wallilabou Falls, 0.6 km E Wallilabou, 55 m [13°14'54.2"N, 61°15'37.7"W], 4 (TTU 105554–55, 105996–97); Wallilabou River Gorge, 0.1 km S, 1.8 km E Wallilabou, 170 m [13°14'31.7"N, 61°15'8.0"W], 2 (TTU 105573–74).

Additional records.—**Charlotte Parish:** Grand Sable Estate (Webster and Handley 1986). **St. George Parish:** Ratho Mill (Timm and Genoways 2003). **St. Patrick Parish:** Lower Bellwood (Timm and Genoways 2003). **No Specific Parish:** no specific locality (Dobson 1878; G. M. Allen 1911; Koopman 1968; Vaughan 1995; Vaughan and Hill 1996).

Specimens captured/released (257).—**Charlotte Parish:** Colonarie River, 1 km S, 2.4 km W South Rivers, 248 m [13°14'10.4"N, 61°09'52.7"W], 19; Fancy River trap, 0.6 km S, 0.3 km E Fancy, 150 m [13°22'31.7"N, 61°08'56.1"W], 12; Golden Grove, 1.5 km N, 2.7 km W Mesopotamia, 410 m [13°13'58.3"N, 61°11'32.7"W], 7; Tunnel, 0.5 km N, 0.9 W Grand Sable, 100 m [13°16'18.3"N, 61°07'42.6"W], 1; 1.2 km N, 2 km W Greiggs, 445 m [13°13'18.2"N, 61°10'42.7"W], 8; La Soufriere Trail, 0.7 km N, 5.1 km W Orange Hill, 646 m [13°19'22.8"N, 61°10'01.2"W], 1; La Soufriere Trailhead, 3.7 km W Orange Hill, 420 m [13°19'00.2"N, 61°09'01.2"W], 3; Montreal trap, 1.5 km N, 1.5 km W Richland Park, 473 m [13°12'30.7"N, 61°11'20.4"W], 24; 0.35 km N, 0.2 km W Old Sandy

Bay, 57 m [13°21'41.4"N, 61°08'07.9"W], 10; Owia Big River Cave, 0.3 km S, 0.3 km W Owia, 97 m [13°22'15.1"N, 61°08'56.1"W], 2; Above Owia, 0.5 km S, 0.3 km W Owia, 172 m [13°22'10.7"N, 61°08'57.1"W], 1; Perseverance, 0.2 km N, 3.1 km W Georgetown, 250 m [13°16'38.7"N, 61°08'52.0"W], 11; Three Rivers Ruins, 93 m [13°14'52.2"N, 61°08'13.2"W], 1; Yambou River Gorge, W Peruvian Vale, 49 m [13°10'16.8"N, 61°09'14.8"W], 44. **St. Andrew Parish:** Lower Buccament River, Buccament, 2 m [13°11'30.2"N, 61°00'16.6"W], 2; Parrot Lookout, Vermont Nature Trail, 2.3 km N, 1.75 km E Vermont, 496 m [13°13'20.2"N, 61°12'43.4"W], 5; Trailhead for Vermont Nature Trail, 1.4 km N, 1.5 km E Vermont, 310 m [13°12'18.8"N, 61°12'53.4"W], 7; Waterworks, 1.25 km N, 1.6 km E Vermont, 310 m [13°12'35.6"N, 61°12'52.0"W], 4. **St. David Parish:** Morgan Woods, 0.4 km N, 2.4 km E Richmond, 253 m [13°18'28.9"N, 61°12'27.9"W], 8; 0.3 km S, 2.2 km E Rose Hall, 435 m [13°15'58.3"N, 61°13'21.9"W], 2; 0.7 km S, 1.75 km E Rose Hall, 379 m [13°15'46.9"N, 61°13'35.4"W], 1; 0.75 km S, 2.3 km E Rose Hall, 377 m [13°15'51.2"N, 61°13'25.7"W], 11. **St. George Parish:** Arnos Vale Factory Ruin, 18 m [13°08'24.3"N, 61°13'43.1"W], 3; Evesham, 155 m [13°10'10.7"N, 61°10'12.9"W], 10; Milikin Bay, near Prospect, 10 m [13°07'59.3"N, 61°10'03.5"W], 37; Mount Pleasant Ruin, 104 m [13°09'02.9"N, 61°09'13.1"W], 1; Mt. St. Andrew, 1.75 km N, 0.3 km E Green Hill, 633 m [13°11'17.9"N, 61°12'56.8"W], 5. **St. Patrick Parish:** Convent, 0.4 km N, 3 km E Grove, 440 m [13°14'53.5"N, 61°12'32.1"W], 3; Wallilabou, 10 m [13°14'54.2"N, 61°16'09.1"W], 5; Wallilabou Falls, 0.6 km E Wallilabou, 55 m [13°14'54.2"N, 61°15'37.7"W], 9.

This long-tongued species was represented in the Lesser Antilles by *G. l. rostrata*, type locality Westerhill Estate, Grenada. Miller (1913a) originally described *rostrata* as a distinct species, with the geographic distribution of Grenada, the Grenadines (Union and Carriacou), and Dominica. He subsequently subsumed this taxon as a subspecies of *longirostris* (Miller 1913b). This taxonomic arrangement has been maintained by recent reviews of the species by Webster and Handley (1986; see also Webster 1993; Webster et al. 1998). They characterized this subspecies from Tobago, Grenada, Grenadines, and St. Vincent as being medium-sized for the species, with a narrow

rostrum, moderately reduced postorbital swellings, a moderately dished facial profile, and zygomatic arches that converge anteriorly. They found specimens from Tobago to be larger overall and those from St. Vincent smaller (Fig. 10).

Mitochondrial DNA sequence data (cytochrome-*b* gene) were made available for *G. longirostris* from St. Vincent, the Grenadines (Union and Carriacou), Grenada, Tobago, and Trinidad by Hoffmann and Baker (2001) and these data indicated that *G. longirostris* and *G. leachi* were sister taxa. These data were limited with respect to our understanding of the molecular systematics of *G. longirostris* because genetic data from *G. longirostris* from northern South America were unavailable for comparison. Nevertheless, within the limited Caribbean geographic sample presented in Hoffmann and Baker (2001) there was useful phylogenetic information with respect to *G. l. rostrata* from Tobago northward and *G. l. major* from Trinidad. In the cytochrome-*b* gene phylogenies the samples of *G.*

longirostris form a distinct clade, but with two subclades corresponding to Trinidad/Tobago and Lesser Antillean (Grenada, Carriacou, Union, and St. Vincent) samples. This phylogeographic structuring indicates genetic isolation between northern (Grenada northward to St. Vincent) and southern (Tobago and Trinidad) Caribbean populations of *G. longirostris*. Thus, with broader genetic sampling, the Tobago population may be found to be more closely related to *G. l. major* of Trinidad, restricting the distribution of *G. l. rostrata* to the Lesser Antillean islands.

Two specimens from Dominica reported by Miller (1913a, 1913b) were shown to be mislabeled individuals from Grenada (Handley and Webster 1987), thereby making St. Vincent the northernmost known population of *G. longirostris*. Probably the first record of *G. l. rostrata* from St. Vincent was a specimen in the British Museum listed as “? Isle of St. Vincent” in Dobson (1878) under the name *Glossophaga soricina*. It was listed under this scientific name because the species *G. longirostris* had not been distinguished and described until 1898. This report may have been the basis of references to “Lesser Antilles” as part of the geographic distribution of *G. l. rostrata* by several subsequent authors (G. M. Allen 1911; Miller 1913a, 1913b).

Table 1 provides the length of forearm and seven cranial measurements for nineteen males and seventeen females from St. Vincent. Males averaged larger (not significantly) than females for length of forearm, zygomatic breadth, and mastoid breadth. Female values averaged larger (not significantly) than males for greatest length of skull, condylobasal length, and length of maxillary tooththrow. Female breadth across the upper molars was significantly ($P=0.04$) larger than values from males. Values for postorbital constriction averaged the same in males and females. Compared to values from Grenada (Genoways et al. 1998), all St. Vincent measurements were within this same range of values except for greatest length of skull, condylobasal length, zygomatic breadth, mastoid breadth, and length of maxillary tooththrow in males, which were smaller, whereas the upper range was larger for breadth across the molars for males. For females the lower ranges were below those for condylobasal length, mastoid breadth, length of maxillary tooththrow, and breadth

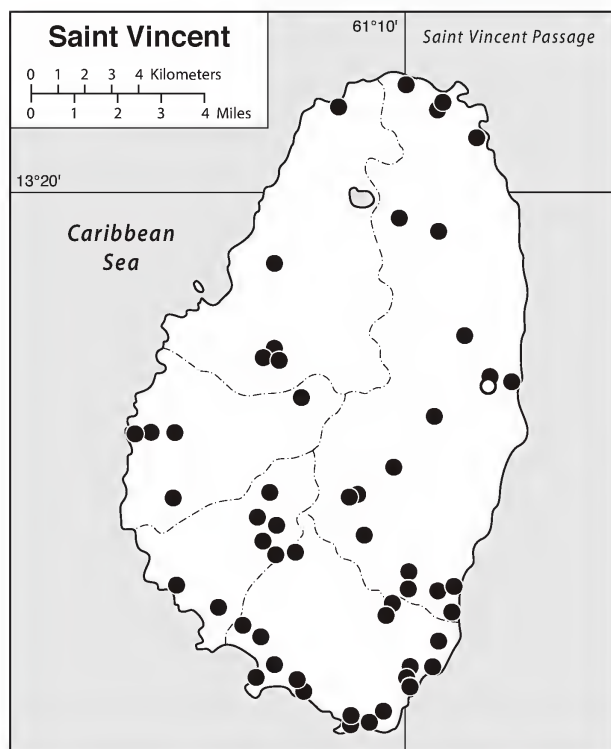


Figure 10. Map of the geographic distribution of *Glossophaga longirostris* on the Lesser Antillean island of St. Vincent. Closed circles represent specimens examined and open circles represent literature records.

across the molars, whereas the upper range values were larger for length of forearm.

Vaughan Jennings et al. (2004) described the echolocation calls of *G. longirostris* from St. Vincent as frequency modulated, of low intensity, and contained at least three harmonics, with the most energy in the third harmonic. They also found that these bats had wings with average aspect ratios, wing tip shape, and wing loading. They concluded that this combination of characters allowed *G. longirostris* to fly slowly in highly cluttered spaces while foraging on pollen and small fruits.

Glossophaga longirostris was one of the two most common and widespread species taken during our surveys on St. Vincent, representing 18.1% of total bat captures. Vaughan and Hill (1996) obtained a similar result on St. Vincent in an ecological survey in which this species constituted 40% of the total 169 captures, being the second-most abundant species in both the banana plantations and rain forests that were sampled. During our research, Miller's Long-tongued Bat was taken in six of 11 day roosts where bats were observed, five of these day roosts being anthropogenic in origin. This species was taken in two human-constructed tunnels—Grand Sable Tunnel and Black Point Cave—and one natural cave—Dennis' Cave. We also list the species as being taken at Owia Big River Cave, even though specimens were netted outside of the cave. *Glossophaga l. rostrata* was captured from near sea level (Buccament River, 2 m) to the highest elevation we netted (646 m, La Soufriere Trail).

Only Miller's Long-tongued Bats were captured in the Arnos Vale Factory Ruin. The ruin was composed of at least three abandoned, vine-covered buildings near the E. T. Joshua Airport. Five specimens were captured using hand nets in a 2-story factory building constructed of sheets of corrugated steel. Considerable light penetrated the building so that seeing the bats was easy.

Black Point Tunnel at Byera Hill housed a large, active colony of *Glossophaga* (Fig. 11). Bats were observed on the ceiling and in alcoves along this dark and windy tunnel that was pushed through 107 m of rock that perforated the Black Point peninsula. During colonial times, this tunnel was used as a warehouse for

the storage of molasses. Another tunnel nearby at 0.5 km N, 0.9 W Grand Sable also served as a day roost for a colony of *G. longirostris* numbering approximately 300 individuals. This second tunnel measured approximately 40 by 2 by 2 m and we were told that it was used as a sleeping tunnel for slaves during colonial times and for transportation of market goods. This tunnel passed through the top of the dry scrub covered Black Ridge that rose 100 m above the Grand Sable River to the north. Here, the river bottom was planted with banana.

Above Rose Hall, we set two nets along the trail leading up from the lower sites to reach this highest elevation site (435 m) that we worked in this area. These nets were situated in a foraging area among secondary rain forest with extensive areas of *Piper* and fig trees; however, only three species were obtained here—*G. longirostris* (3), *M. plethodon* (2), and *A. schwartzi* (7).



Figure 11. Photograph of the entrance of Black Point Tunnel, Charlotte Parish, St. Vincent. This man-made tunnel housed a large colony of Miller's Long-tongued Bats, *Glossophaga longirostris*.

Males taken on 5 May and 18 May had testes lengths of 6 and 7, respectively. One hundred and six females were examined in the period of 21 May to 6 June during the transition period between the dry season and beginning of the wet season. Forty-eight of these females were pregnant of which 13 had embryos that averaged 14.5 (10–20). Among the remaining females 34 were lactating, two were post-lactating, and 22 revealed no gross reproductive activity, one of which was a juvenile taken on 26 May 2006. Eighty-nine males were examined during this time period, with 75 individuals having testes lowered into the scrotum and 14 having testes retracted into an inguinal position. The mean length of testes of 11 of the scrotal individuals was 3.6 (2.5–4.0), whereas the mean testes length of seven males with non-scrotal testes was only slightly shorter, 3.4 (2.0–5.0). A young male taken on 5 June 2006 had unfused phalangeal epiphyses. Eighty-three females were examined in the period of 27 July to 8 August in the height of the wet season. A total of 49 of these females revealed no gross reproductive activity, 14 were post-lactating, 12 were lactating, and five were pregnant carrying a single embryo. Three taken on 1 and 3 August 2005 were judged to be juveniles based on their open phalangeal epiphyses. Sixty-three males were examined during this time period, with 26 individuals having scrotal testes and 37 having testes retracted into an inguinal position. The mean length of testes of 12 of the scrotal individuals was 5.6 (3.0–8.0), whereas the mean length of testes of eight of the non-scrotal individuals was 3.0 (2.0–4.0). One young male taken on 4 August 2005 had unfused phalangeal epiphyses. On 23–24 August 1967, 12 adult females were obtained of which eight were pregnant, whereas the other four revealed no gross reproductive activity. The eight embryos had a mean crown-rump length of 17.9 (11.0–23.0). Eight adult males taken on these dates had an average testes length of 3.3 (3.0–6.0). Of the female bats captured early in the dry season, one female was pregnant and another carried a non-volant juvenile on 25 December 1961, and a reproductively inactive female was captured on 28 December 1961.

In sum, our St. Vincent data matches those from Grenada and the Grenadines in that these insular bat populations are reproductively active at the beginning of the dry season (December), in the transition from the dry season to the wet season (May and June), and

into the height of the wet season (July and August) (Genoways et al. 1998, 2010). There were also reproductively inactive females in the population at these times. It was difficult to name this reproductive cycle, but trimodal polyestry or aseasonal polyestry would most closely match the existing data. It was clear that this was a highly successful reproductive scheme that resulted in high population numbers on these southern Lesser Antillean islands.

In late May and early June, 18 pregnant females had an average weight of 14.8 (11.1–17.0), 16 lactating females averaged 11.7 (9.9–13.8), 12 non-reproductive females averaged 11.2 (8.8–12.7), and a juvenile female weighed 5.6. During this period 34 males with testes in scrotal position had an average weight of 11.2 (9.5–13.4), whereas 10 males with testes in a non-scrotal position weighed on average 10.4 (9.3–11.6). In late July and early August, seven lactating females had a mean weight of 10.3 (9.2–13.1), nine non-reproductive females had a mean weight of 10.1 (8.1–12.3), four post-lactating females had a mean weight of 10.8 (10.2–11.6), and a juvenile female had a weight of 7.8. Six males from this period with testes in scrotal position had a mean weight of 11.3 (10.5–11.8), whereas seven males with testes in an inguinal position had a mean weight of 10.7 (8.0–13.2).

***Brachyphylla cavernarum cavernarum* Gray, 1834**
Antillean Fruit-eating Bat

Specimens examined (75).—**Charlotte Parish:** Montreal trap, 1.5 km N, 1.5 km W Richland Park, 473 m [13°12'30.7"N, 61°11'20.4"W], 1 (TTU 105669); Owia Big River Cave, 0.3 km S, 0.3 km W Owia, 97 m [13°22'15.1"N, 61°08'56.1"W], 21 (TTU 105389–99, 105697–706). **St. Andrew Parish:** Bat Cave, 0.75 km S, 0.5 km W Buccament, 0 m [13°11'10.6"N, 61°16'15.2"W], 15 (TTU 105721–35); Parrot Look-out, Vermont Nature Trail, 2.3 km N, 1.75 km E Vermont, 496 m [13°13'20.2"N, 61°12'43.4"W], 1 (TTU 105770); Petroglyph site, Pembroke, ca. 1 mi. W Cane Grove, 3 (NMNH 580677, 580714–15). **St. George Parish:** Clifton Hill, 400 ft., 2 (KU 110151–52); Kingstown, 150 ft., 1 (KU 110153). **No Specific Parish:** no specific locality, 31 (NMNH 106056–73, 106075, 106077–81, 106083–89).

Additional records.—**St. George Parish:** Clifton, 400 ft. (Swanepoel and Genoways 1978); Kingstown, 150 ft. (Swanepoel and Genoways 1978). **St. Patrick Parish:** near Barrouallie (G. M. Allen 1911). **No Specific Parish:** no specific locality (Gray 1834; Dobson 1878; Miller 1913a; Koopman 1968; Swanepoel and Genoways 1978; Jones 1989; Vaughan 1995; Vaughan and Hill 1996).

Specimens captured/released (38).—**Charlotte Parish:** Owia Big River Cave, 0.3 km S, 0.3 km W Owia, 97 m [$13^{\circ}22'15.1''\text{N}$, $61^{\circ}08'56.1''\text{W}$], 13; Above Owia, 0.5 km S, 0.3 km W Owia, 172 m [$13^{\circ}22'10.7''\text{N}$, $61^{\circ}08'57.1''\text{W}$], 25.

This genus and species were originally described by J. E. Gray (1834) based on material in the British Museum (Natural History) submitted by “the late Rev. Lansdown Guilding.” According to Rev. Guilding: “This Bat inhabits caves in St. Vincent’s . . .” There is some confusion about what is the correct year of Mr. Gray’s official description of this new species. The initial notification of this new species was a reading of the description before a meeting of the Zoological Society of London on 26 November 1833, but it was not until 12 March 1834 that the printed version of the description appeared. It was on the latter date that the name became official.

The genus *Brachyphylla* was most recently revised by Swanepoel and Genoways in 1978. It is endemic to the Antilles with two species currently recognized. The northern species, *B. nana*, occurs on Cuba, Grand Cayman, Middle Caicos, and Hispaniola. The larger species, *B. cavernarum*, is known from Puerto Rico, the Virgin Islands, and the Lesser Antillean islands as far south as St. Vincent and Barbados (Fig. 12). Bats of the nominate subspecies are the largest of the species and occur on St. Croix and throughout the Lesser Antilles south to St. Vincent, with the exception of Barbados where small-sized individuals of *B. c. minor* occur (Genoways et al. 2011). The third subspecies, *B. c. intermedia*, is found on Puerto Rico and all Virgin Islands except St. Croix (Swanepoel and Genoways 1978). Although a formal analysis of the molecular systematics and population genetics of southern Lesser Antillean populations of *B. cavernarum* remains to be conducted, Carstens et al. (2004) show a lack of genetic variation across individuals collected from

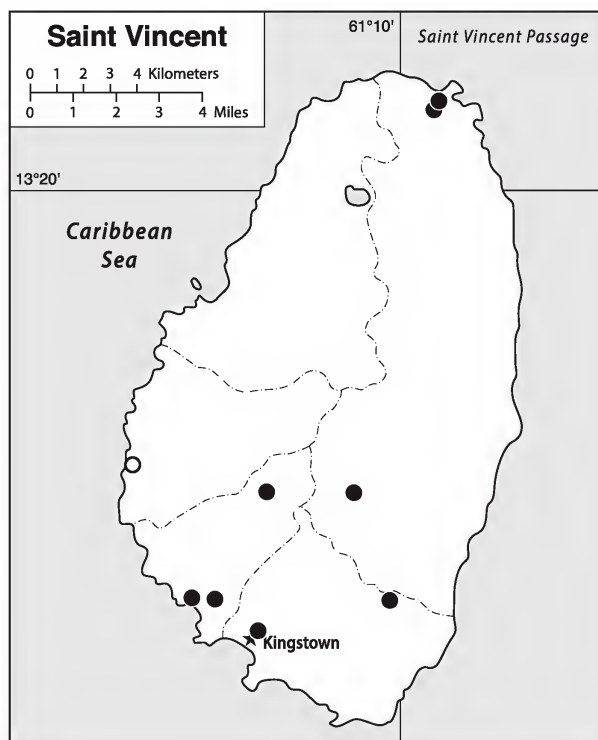


Figure 12. Map of the geographic distribution of *Brachyphylla cavernarum* on the Lesser Antillean island of St. Vincent. Closed circles represent specimens examined and open circles represent literature records.

northern Lesser Antillean populations. We searched for *Brachyphylla* throughout the Grenadine islands without success. However, from a point on Bequia, we could see the area where a *Brachyphylla* colony was located on St. Vincent—Bat Cave (Genoways et al. 2010).

Forearm measurements (Table 1) from 20 females and 24 males fall within ranges of samples examined by Swanepoel and Genoways (1978) except for one female that exceed the range (69.8 versus 69.0 in current sample). Females averaged slightly larger than males for length of forearm, greatest length of skull, condylobasal length, zygomatic breadth, length of mandibular tooththrow, and breadth across upper molars, whereas there were no differences in the average values for postorbital constriction and mastoid breadth. No statistically significant secondary sexual variation was found in our sample, which conforms to results found by Swanepoel and Genoways (1978) for *B. cavernarum* in the Lesser Antilles.

Bats of this species have been reported to find day roosts in caves, rock crevices, rock overhangs, old disused buildings, dense tree tops, and in underground, unused human-made structures, and not always where it was dark (Bond and Seaman 1958; Swanepoel and Genoways 1978, 1983). We found only cave day roosts for *B. cavernarum* on St. Vincent. The majority of our specimens came from caves (Owia Big River Cave and Bat Cave, near Buccament), whereas netting in forests or other foraging sites resulted in only two other captures—one at 496 m (Parrot Lookout, Vermont Trail) and one at the Montreal Trap (473 m) (Fig. 13).

Bat Cave was located on the leeward coast of the island just south of the mouth of the Buccament River. The cave was little more than a cylindrical vertical pocket in a protruding ridge of compacted volcanic material, which was formed by wave action scouring

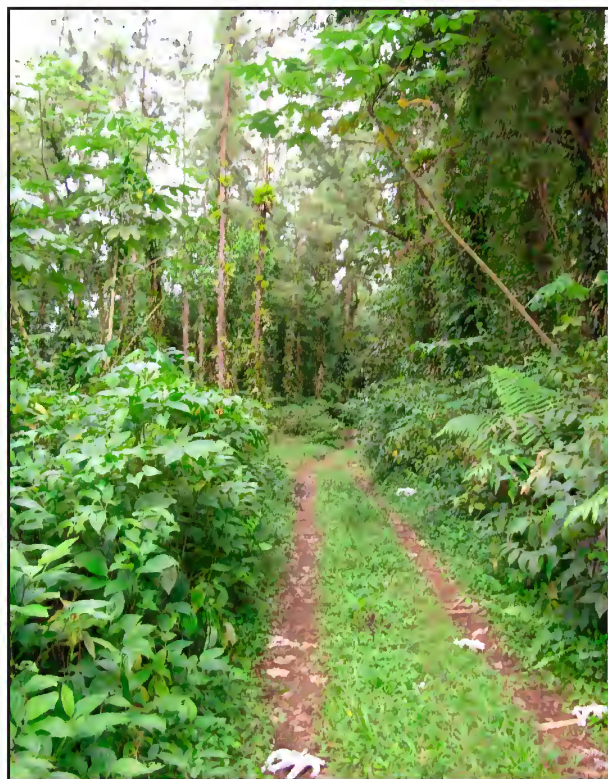


Figure 13. Photograph of part of the field site at Montreal Trap, Charlotte Parish, St. Vincent. The trail leads through part of a Caribbean pine, *Pinus caribaea*, plantation at approximately 473 meters. This was one of two places where a *Brachyphylla cavernarum* was captured at a foraging site.

the surfaces of the cave. The floor of the cavity was filled with water about 1.5 m deep with a sandy bottom, with no haul out points above the water level. The cavity above the waterline extended about 3 m and was roughly oblong with the same dimensions. The bats roosted along the walls, moving to the dome only when disturbed. During our team's visit to the cave no more than 20 bats, all believed to be *B. cavernarum*, were observed. A second species reportedly has been observed in the cave, which was probably *N. leporinus*. The second day roost site for this species was the Owia Big River Cave described in the account for *P. fuscus*.

When Austin H. Clark traveled to the island in 1903, he thought that the large cave near Barrouallie was the only place that the *B. cavernarum* occurred on St. Vincent. Clark wrote to G. M. Allen (1911) that the cave was "a rather large chamber with two entrances, one at about the high-water mark, and rather low; the other about ten feet in height, through which a boat may be rowed. He saw but two bats, both of which were secured, and proved to be of this species. A few years before, a collector who visited this spot, obtained a large number; and the bats appear to subsequently to have left."

One of the two foraging sites where we obtained *B. cavernarum* was Parrot Lookout along the Vermont Nature Trail. The nature reserve covers an area of 4,400 ha composed primarily of tropical lowland rainforest. The Lookout was situated on a ridge top near the boundary of the reserve, with a very narrow path leading to the top and then running along the ridge top where a strong breeze was blowing from north to south. Eleven mist nets were set perpendicular and parallel to this trail, in areas with such notable flora as pepper plant, candlewood, galba, wild red ginger, big leaf santinay, white cinnamon, ashes wood, black fig, trumpet tree, helecho gigante, heliconias, wild mahoe, chaste tree, and fiddlewood. Here we caught seven species of bats, including one *B. cavernarum* taken near the buttresses of a helecho gigante and not far from a waterwood tree. Individuals of *Micronycteris* also were taken in this area, but the most abundant species was *Monophyllus*, which was represented by 30 individuals.

On 5 June 2006, we captured 47 adult *B. cavernarum* in the Owia Big River Cave and the Above Owia

site at the northern end of the island. Of these individuals, 13 were males that evinced no gross reproductive activities, having their testes in an inguinal position. The average testes lengths of five *B. cavernarum* were 4.6 (2.0–6.0). The 34 females were all lactating, but none presented any evidence of post-partum breeding. One unfurred pup had a length of forearm of 50.0 and a weight of 18.4 as compared with its mother, 66.0 and 42.3. We had visited these caves previously on 27 July 2005, taking a sample of five males and five females. Only one of the females was lactating and revealed no other reproductive activity. The remaining nine individuals were non-reproductive and based on their weights were probably flying young of the year, with adult length of forearm measurements. The five males had a mean testes length of 3.5 (3.0–4.0). On 6 August 2005 we visited Bat Cave near the southern end of the island from which we obtained 15 Antillean fruit-eating bats—nine females and six males. Five of the females were lactating and three were judged to be post-lactating based on the fact that the bats' nipples were enlarged with a hairless area around the base, but no milk could be palpated from the nipple. The remaining female evinced no reproductive activity. None of the males evinced reproductive activity, having their testes in an inguinal position. Based on their lower weights, two of these individuals may have been flying young of the year. Length of testes of four males averaged 4.5 (4.0–5.0). The testes lengths of two bats taken on 22–23 August 1967 were 4 and 6.

Although the reproductive data from our study cover less than three months, they do give some important insights into the reproductive cycle of the *B. cavernarum*. Spermatogenesis has been observed in males from September to December on St. Croix (Krutzh and Nellis 2006) and males on St. Vincent were not reproductively active 5 June to 23 August. The reproductive cycle of females was synchronized seasonal monoestry because all young had been born prior to 5 June. Females apparently do not undergo post-partum estrus as none were found carrying an embryo later than in early June. These reproductive data conform closely to those of other populations of *B. cavernarum*. Elsewhere in their geographic range, pregnant (single young) females have been reported from February to June and lactating females have been found from April through July (Hayssen et al. 1993).

The 13 males from the two sites south of Owia taken in early June weighed on average 45.6 (40.5–53.5), whereas 20 lactating females taken here averaged a weight of 44.2 (38.0–49.1). The lactating adult taken at Owia Big River Cave on 27 July weighed 41.6, the five young of the year males averaged 32.4 (27.8–38.0), and the four young females had a mean weight of 29.8 (25.5–34.5). Among the females taken on 6 August at Bat Cave, the five lactating females had a mean weight of 48.6 (45.0–54.0), three post-lactating individuals weighed 44.6, 46.3, and 48.1, and a non-reproductive female weighed 40.9. Six males taken at Bat Cave had a mean weight of 43.5 (39.4–48.7).

Sturnira paulsoni paulsoni de la Torre and
Schwartz, 1966

Paulson's Yellow-shouldered Bat

Specimens examined (82).—**Charlotte Parish:** Colonarie River, 1 km S, 2.4 km W South Rivers, 248 m [13°14'10.4"N, 61°09'52.7"W], 2 (TTU 105653–54); Fancy River trap, 0.6 km S, 0.3 km E Fancy, 150 m [13°22'31.7"N, 61°08'56.1"W], 3 (TTU 105661–63); 1.2 km N, 2 km W Greiggs, 445 m [13°13'18.2"N, 61°10'42.7"W], 2 (TTU 105314–15); Golden Grove, 1.5 km N, 2.7 km W Mesopotamia, 410 m [13°13'58.3"N, 61°11'32.7"W], 2 (TTU 105338–39); La Soufriere Trail, 0.7 km N, 5.1 km W Orange Hill, 646 m [13°19'22.8"N, 61°10'01.2"W], 3 (TTU 105362–64); La Soufriere Trailhead, 3.7 km W Orange Hill, 420 m [13°19'00.2"N, 61°09'01.2"W], 2 (TTU 105381–82); 3.2 km N, 2.2 km W Mesopotamia, 1 (CM 83403); Montreal trap, 1.5 km N, 1.5 km W Richland Park, 473 m [13°12'30.7"N, 61°11'20.4"W], 17 (TTU 105676–89, 105694–96); 1 km S Peruvian Vale, 2 (CM 83404–05); Richmond Hill, 1 (ROM 60164); Yambou River Gorge, W Peruvian Vale, 49 m [13°10'16.8"N, 61°09'14.8"W], 6 (TTU 105461–66). **St. Andrew Parish:** Lower Buccament River, Buccament, 2 m [13°11'30.2"N, 61°00'16.6"W], 1 (TTU 105757); Lowrt [=Lowrey], 1000 ft., 1 (NMNH 361882); Mt. St. Andrew, 0.35 km S, 3.0 km E Pembroke, 501 m [13°11'12.6"N, 61°13'07.0"W], 2 (TTU 109113–14); Parrot Lookout, Vermont Nature Trail, 2.3 km N, 1.75 km E Vermont, 496 m [13°13'20.2"N, 61°12'43.4"W], 1 (TTU 105807); Trailhead for Vermont Nature Trail, 1.4 km N, 1.5 km E Vermont, 310 m [13°12'18.8"N, 61°12'53.4"W], 4 (TTU 105812–15); Vermont Nature

Trail, 1.6 mi E Vermont (by road), 2 (NMNH 580674, 580708); Petroglyph site, Pembroke, ca. 1 mi. W Cane Grove, 1 (NMNH 580709); Waterworks, 1.25 km N, 1.6 km E Vermont, 310 m [13°12'35.6"N, 61°12'52.0"W], 2 (TTU 105476–77). **St. David Parish:** Falls of Baleine, 13 km S, 2.6 km W Fancy, 130 m [13°22'13.6"N, 61°11'36.2"W], 1 (TTU 105523); Morgan Woods, 0.4 km N, 2.4 km E Richmond, 253 m [13°18'28.9"N, 61°12'27.9"W], 2 (TTU 105542–43); 0.7 km S, 1.75 km E Rose Hall, 379 m [13°15'46.9"N, 61°13'35.4"W], 2 (TTU 105502–03); 0.75 km S, 2.3 km E Rose Hall, 377 m [13°15'51.2"N, 61°13'25.7"W], 1 (TTU 105511). **St. George Parish:** 1.3 km N, 2.7 km E Calliagua, 2 (CM 83406–07); Calliagua, 1 (AMNH 219147); Clifton Hill, 400 ft., 6 (KU 110142–47); Milikin Bay, near Prospect, 10 m [13°07'59.3"N, 61°10'03.5"W], 1 (TTU 105955); Mt. St. Andrew, 1.75 km N, 0.3 km E Green Hill, 633 m [13°11'17.9"N, 61°12'56.8"W], 2 (TTU 105549–50). **St. Patrick Parish:** Convent, 0.4 km N, 3 km E Grove, 440 m [13°14'53.5"N, 61°12'32.1"W], 3 (TTU 105977–79); Wallilabou Falls, 0.6 km E Wallilabou, 55 m [13°14'54.2"N, 61°15'37.7"W], 2 (TTU 105559, 106000); Wallilabou River Gorge, 0.1 km S, 1.8 km E Wallilabou, 170 m [13°14'31.7"N, 61°15'8.0"W], 4 (TTU 105577–80).

Additional records.—**St. Andrew Parish:** Lowrt [=Lowrey], 1000 ft. (de la Torre and Schwartz 1966; Timm and Genoways 2003). **No Specific Parish:** no specific locality (Vaughan 1995; Vaughan and Hill 1996).

Specimens captured/released (98).—**Charlotte Parish:** Fancy River trap, 0.6 km S, 0.3 km E Fancy, 150 m [13°22'31.7"N, 61°08'56.1"W], 1; 1.2 km N, 2 km W Greiggs, 445 m [13°13'18.2"N, 61°10'42.7"W], 4; Golden Grove, 1.5 km N, 2.7 km W Mesopotamia, 410 m [13°13'58.3"N, 61°11'32.7"W], 6; La Soufriere Trail, 0.7 km N, 5.1 km W Orange Hill, 646 m [13°19'22.8"N, 61°10'01.2"W], 2; La Soufriere Trailhead, 3.7 km W Orange Hill, 420 m [13°19'00.2"N, 61°09'01.2"W], 7; Montreal trap, 1.5 km N, 1.5 km W Richland Park, 473 m [13°12'30.7"N, 61°11'20.4"W], 12; Perseverance, 0.2 km N, 3.1 km W Georgetown, 250 m [13°16'38.7"N, 61°08'52.0"W], 4. **St. Andrew Parish:** Parrot Lookout, Vermont Nature Trail, 2.3 km N, 1.75 km E Vermont, 496 m [13°13'20.2"N, 61°12'43.4"W], 2; Trailhead for Vermont Nature Trail,

1.4 km N, 1.5 km E Vermont, 310 m [13°12'18.8"N, 61°12'53.4"W], 4; Waterworks, 1.25 km N, 1.6 km E Vermont, 310 m [13°12'35.6"N, 61°12'52.0"W], 2. **St. David Parish:** Morgan Woods, 0.4 km N, 2.4 km E Richmond, 253 m [13°18'28.9"N, 61°12'27.9"W], 20; 0.7 km S, 1.75 km E Rose Hall, 379 m [13°15'46.9"N, 61°13'35.4"W], 7; 0.75 km S, 2.3 km E Rose Hall, 377 m [13°15'51.2"N, 61°13'25.7"W], 3. **St. Patrick Parish:** Convent, 0.4 km N, 3 km E Grove, 440 m [13°14'53.5"N, 61°12'32.1"W], 20; Wallilabou River Gorge, 0.1 km S, 1.8 km E Wallilabou, 170 m [13°14'31.7"N, 61°15'8.0"W], 4.

Bats of the genus *Sturnira* are known in the Lesser Antilles from Montserrat (Pedersen et al. 1996) southward to Grenada (Genoways et al. 1998), but are absent from Barbados (Genoways et al. 2011) and the Grenadines (Genoways et al. 2010). Traditionally two species have been known from the Lesser Antilles—*S. thomasi*, with two subspecies, found on Montserrat and Guadeloupe, and *S. lilium*, with six recognized subspecies, found from Dominica to Trinidad and the South American mainland (Genoways 1998). The first specimen of *Sturnira* from St. Vincent was collected by D. R. Paulson in 1961. This became the basis of the name *S. paulsoni* when first described (de la Torre and Schwartz 1966), but subsequently it was reassigned as a subspecies of the widespread mainland species *S. lilium* (Jones and Phillips 1976). However, recent molecular studies of the members of the *Sturnira* “*lilium*” group have questioned this systematic arrangement and formed the basis for a strikingly new arrangement.

Velazco and Patterson (2013) provided statistically supported genetic data to recognize a single species in the southern Lesser Antilles distributed from Grenada northward to St. Lucia to which the name *Sturnira paulsoni* was applied. In the northern Lesser Antilles from Montserrat to Martinique, Velazco and Patterson (2013) recognized a second endemic species *Sturnira angeli*, which probably invaded the Caribbean ~1.5 million years ago and has been isolated there. The previously recognized species *Sturnira thomasi*, endemic to Guadeloupe and Montserrat, was subsumed under *S. angeli* because their data did not separate populations on Dominica/Martinique from those on Guadeloupe/Montserrat. Velazco and Patterson (2013) considered the species occurring from Tobago, Trini-

dad, and northern South America to be undescribed and lacking a scientific name. Their data suggested either two separate invasions into the Caribbean (by *Sturnira angeli* and *Sturnira paulsoni*), or one invasion into the Caribbean followed by re-invasion to the mainland. This latter suggestion was because *S. luisi* known from the Chocó of Panama and Ecuador was a clade (with moderate statistical support) that was sister to *S. paulsoni*. Velazco and Patterson (2013) restricted the use of the name *Sturnira lilium* to populations occurring in the area of the Brazilian Shield in southern Brazil, whereas it previously had been broadly applied to populations of yellow-shouldered bats across Mexico, Central America, northern South America, and into the Caribbean. The distinct morphological characters of subspecies represented local adaptation/isolation on each of the islands resulting in the following revised taxonomy (listed from north to south): Montserrat, *Sturnira angeli vulcanensis* Genoways, 1998; Guadeloupe, *Sturnira angeli thomasi* de la Torre and Schwartz, 1966; Dominica, *Sturnira angeli angeli* de la Torre, 1966; Martinique, *Sturnira angeli zygomaticus* Jones and Phillips, 1976; St. Lucia, *Sturnira paulsoni luciae* Jones and Phillips, 1976; St. Vincent, *Sturnira paulsoni paulsoni* de la Torre and Schwartz, 1966; and Grenada, *Sturnira paulsoni serotinus* Genoways, 1998.

As noted previously, the traditional taxonomic arrangement of Antillean *Sturnira* was based on morphometric and morphological characteristics and resulted in the recognition of an endemic species—*S. thomasi* on Guadeloupe and Montserrat—and a mainland species—*S. lilium* distributed from northern South America and Trinidad northward to Dominica (de la Torre 1966; de la Torre and Schwartz 1966; Jones and Phillips 1976; Genoways 1998). This much discordance between molecular and morphological data is not unique, but it is unusual. There were two major breaks in the molecular data between South America-Trinidad and Grenada and between St. Lucia and Martinique, whereas there was only one break in the morphological data between Dominica and Guadeloupe. The morphometric break was illustrated by the non-overlapping of the length of forearm measurements of adult *S. thomasi* in which the shortest forearm was 45.9, whereas the longest length of forearm of populations from Dominica south to Trinidad was 45.2 (Genoways and Jones 1975; Genoways 1998). The shape of the crania of bats from

Dominica southward were variations on the shape of the crania of bats from Trinidad—medium-size for the genus and the proportions of length and breadth of the crania did not vary significantly among populations. The crania of bats from Guadeloupe and Montserrat varied from these proportions with a remodeling resulting in crania that were longer and narrower than the southern populations. This change in proportions was well illustrated by the greatest length of skull measurements in which the smallest *S. thomasi* was 24.9 and the largest in the southern populations was 23.7, whereas the measurements for zygomatic breadth were reversed in size with *S. thomasi* being 12.7 and smaller and the other populations being 12.7 or larger. Populations on Guadeloupe and Montserrat had a tendency to be missing m3, which was present in southern populations. As we have seen with *Artibeus* populations, the presence/absence of molars can be a species-level character or simply a polymorphism. The cuspids on m1 also differed, although the southern populations displayed two morphological types—in bats from Grenada, St. Vincent, and St. Lucia (corresponding to *S. paulsoni*) the paraconid was positioned on the lingual edge of the tooth so that the paraconid, metaconid, and entoconid form a linear lingual sequence and the entoconid was enlarged, whereas in populations from Trinidad, Martinique, and Dominica the paraconid was located nearer the center line of the tooth so it did not form a linear sequence with the metaconid and entoconid and the entoconid was only a low ridge. In the populations from Guadeloupe and Montserrat these cuspids form a third pattern—the paraconid, metaconid, and entoconid were distinct, but the paraconid was low and extended forward as a low ledge, with metaconid and entoconid well developed and connected by a commissure (de la Torre 1966; de la Torre and Schwartz 1966; Jones and Phillips 1976; Genoways 1998). Although this discordance in datasets can be viewed as a scientific problem, we view it as an opportunity in need of further research to gain a deeper understanding of the relationships among these Antillean populations of *Sturnira*. We have followed the taxonomy of the molecular study (Velazco and Patterson 2013) because it was comprehensive and most recently conducted. However, we recommend additional genomic analyses aimed at characterizing microevolutionary processes, including putative incipient speciation events (see *Ardops nicholli* account below).

Length of forearm and seven cranial measurements of 15 males and 15 females (Table 1) of *S. p. paulsoni* were examined for secondary sexual dimorphism. Males were significantly ($P \leq 0.01$) larger than females for greatest length of skull, condylobasal length, zygomatic breadth, mastoid breadth, and breadth across the upper molars. Males were also significantly larger ($P = 0.019$) than females for length of the maxillary toothrow. Although male length of forearm and mastoid breadth averaged larger than females, there was no significant difference between the sexes. The mean for postorbital constriction measurements was the same for both sexes.

Vaughan Jennings et al. (2004) found the echolocation calls of *S. paulsoni* from St. Vincent were frequency modulated, of low intensity, and contained at least four harmonics, with the most energy in the second harmonic. They also found that these bats had wings with average aspect ratios, average wing tip index, and high wing loading. Vaughan Jennings et al. (2004) concluded that this combination of characters allowed *S. paulsoni* to have good turning flight in clutter, as well as achieving fast and efficient commuting flight in open space.

This bat was captured at 24 net sites and represented 8.3% of total captures (Fig. 14). Most often the greatest numbers were taken in nets placed across trails through forests, plantings, or across streams. We worked two sites on Mt. St. Andrew, with the site at 1.75 km N, 0.3 km E Green Hill being the higher elevation of the two at 633 m. The grade of the road leading up the peak was very steep and at the site where we conducted our collecting there was an approximately 30-m high cliff face on one side and a drop of similar size just off the other side of the road. We set three nets across and along the road. The vegetation was thick and difficult to penetrate given the cliffs. Our nets were set by 1900 hr. In addition to two *S. paulsoni* we caught 13 *A. schwartzi*, one *M. buriri*, and seven *G. longirostris*. The fog rolled in at about 2150 hr, making bat activity very low and as it began to rain quite heavily at 2250 hr, we took down the nets.

The Fancy Trap locality was situated around a catchment in the Fancy River to provide water of additional quantity and quality for the town of Fancy

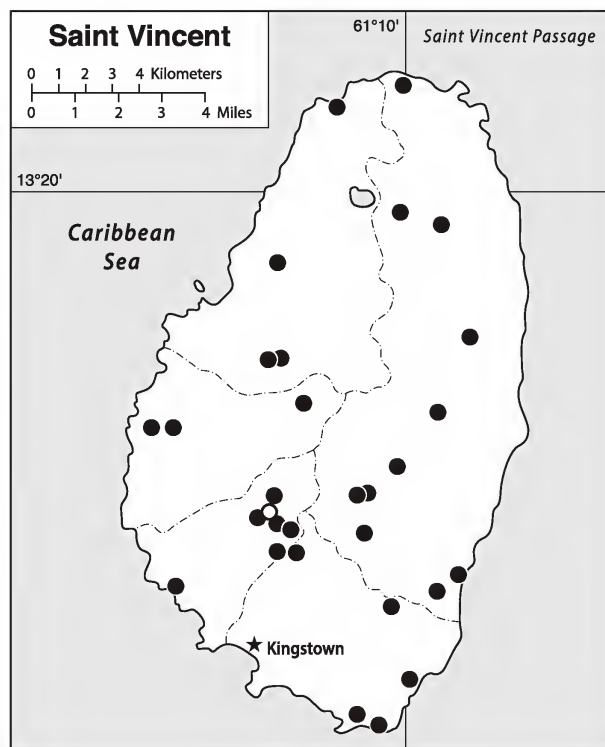


Figure 14. Map of the geographic distribution of *Sturnira paulsoni* on the Lesser Antillean island of St. Vincent. Closed circles represent specimens examined and open circles represent literature records.

and surrounding agricultural lands at the extreme northern end of the island (Fig. 15). The catchment was sited near the point where stands of early succession secondary rain forest came down the north slope of the La Soufriere volcano to meet the agricultural lands from lower elevations around the town and the coast. The agricultural lands near where we worked were dominated by fields of dasheen and groves of oil palms, whereas the early succession secondary rain forest was dominated by such trees species as mango, pepper plant, manjack, Spanish ash, white cinnamon, trumpet tree, helecho gigante, wild mahoe, and fiddlewood. One mist net was set at the boundary between the agricultural lands and forest and another five nets were placed within the forest and across the river. All nets captured individuals of *A. schwartzi*, while a net set in a large patch of *Piper* caught two *S. paulsoni* as well as *G. longirostris* and *A. nichollsi*. An additional two specimens of *S. paulsoni* were taken in a net set in a small opening in the forest not far from the river.



Figure 15. Photograph of field site at Fancy Trap, Charlotte Parish, St. Vincent. The photograph was taken looking to the south at the northern slope of La Soufriere. The upper slopes remain in tropical forest, whereas the lower slopes have been converted for agricultural purposes. Four individuals of Paulson's Yellow-shouldered Bats, *Sturnira paulsoni*, as well as *G. longirostris*, *A. schwartzi*, and *Ardops nichollsi*, were captured at this site.

The Rose Hall work site at 379 m was located only a short distance from the Rose Hall site at 377 m discussed in the *M. plethodon* account. As opposed to the 377 m site where the habitat was relatively open with a variety of fruiting trees, the habitat at the 379 m site was closed with dense secondary rain forest. Three nets, which were placed across the trail leading through the forest, caught nine *S. paulsoni*, one *P. fuscus*, three *G. longirostris*, and eight *A. schwartzi*. Comparing the bats captured at 379 m site with the 377 m site, they shared three species (*G. longirostris*, *A. schwartzi*, *S. paulsoni*), whereas 379 m had one unique species (*P. fuscus*) and 377 m had two unique species (*M. buriri*, *M. plethodon*). In addition to these differences, only a single Paulson's Yellow-shouldered Bat was netted at 377 m, whereas nine were taken at 379 m.

We have reproductive data for *S. paulsoni* on St. Vincent from the end of the dry season and the beginning of the rainy season (24 May–6 June) and the height of the rainy season (27 July–6 August), with July being the wettest month of the year. During the first of these periods, 56 of the 72 females for which we have data were lactating. Of the remainder, one female was lactating and pregnant and seven were pregnant with

single embryos, one of which measured 21 in crown-rump length. One female was post-lactating and six evinced no gross reproductive activity. We netted one volant young female with a length of forearm of 42.0 and a weight of 13.0. Ten males with testes in a scrotal position had a mean testes length of 6.1 (4.5–7.5). The rainy season sample of 60 females included 27 that exhibited no gross reproductive activity, 10 that were post-lactating, and four that were lactating. Seventeen additional females were pregnant each of which carried a single embryo, one of which measured 11 in crown-rump length. A juvenile female taken on 28 July 2005 weighed 12.3. Fourteen of the male *S. paulsoni* from the period at the end of the dry season to the beginning of rainy season had testes in the scrotal position. Two of these males had a testes length of 5 and 6. Ten males with testes in an inguinal position from the height of the rainy season had testes lengths that averaged 4.9 (3–9), whereas 13 additional males simply were judged to be in a non-reproductive state.

Wilson (1979) found that mainland populations of closely related yellow-shouldered bats follow a bimodal polyestrous reproductive cycle and the data for the St. Vincent population of *S. paulsoni* appears to fit this pattern. Most females had undergone parturition before our work started in late May, with nearly 80% of them lactating. At this time, six bats were pregnant suggesting that *S. paulsoni* bring off their young just at the beginning of the wet season on St. Vincent. The males also appeared to be reproductively active at this time. A postpartum estrus may be occurring, as one female was lactating and pregnant on 28 May. By the height of the rainy season in late July and early August, 30% of the females were pregnant, four were lactating, and 10 were post-lactating, but about 43% of females showed no gross reproductive activity so the postpartum breeding did not include the entire population. The males at this point were becoming reproductively inactive.

During the May–June period, 31 lactating females weighed on average 18.1 (16.8–21.0), four pregnant females averaged 22.6 (17.0–24.9) in weight, two non-reproductive females weighed 16.8 and 18.7, and a female that was pregnant and lactating weighed 18.4. Fourteen males from this time period had a mean weight of 20.5 (18.0–22.6). During the July–August period,

12 non-reproductive females weighed on average 16.7 (14.2–19.5), whereas nine pregnant females had a mean weight of 18.9 (15.7–23.8). Seven males from this time period had a mean weight of 19.0 (15.7–23.8).

Artibeus lituratus palmarum J. A. Allen and
Chapman, 1897
Greater Fruit-eating Bat

Specimens examined (3).—**Charlotte Parish:** 0.35 km N, 0.2 km W Old Sandy Bay, 57 m [13°21'41.4"N, 61°08'07.9"W], 2 (TTU 105292–93). **St. George Parish:** Clifton Hill, 400 ft., 1 (KU 110181).

Additional records.—**St. George Parish:** Jones and Phillips (1970), no specific locality in publication, but deposited at KU110181, Clifton Hill, 400 ft.

We caught two males of *A. lituratus* on our penultimate night of netting on 5 June 2006 (24th night of netting) at Old Sandy Bay, Charlotte Parish, elevation 57 m. These were the second and third specimens of this species captured on St. Vincent (Fig. 16). The first individual was reported by Jones and Phillips (1970) based on a skull-only specimen from Clifton Hill (Koopman 1989 agreed with this identification). Populations of *A. lituratus* were found to be sympatric with *Artibeus schwartzi* on three islands in the Grenadines (Genoways et al. 2010) and were widespread on Grenada (Genoways et al. 1998) where it was taken at several sites along with its more abundant congener *Artibeus planirostris* (Genoways et al. 1998). The genus *Artibeus* is the only one with two species represented on St. Vincent. It seemed to us (Genoways et al. 2010) that it was improbable for two large frugivorous species to co-exist on the small, arid Grenadine islands, but they are sympatric on three. Therefore, it was not overly surprising to find them together on the much larger and lush island of St. Vincent, but nevertheless the population levels of *A. lituratus* seem small.

By the time we captured these two *A. lituratus*, we had sorted over 900 *Artibeus* and always worried that we had missed this species. However, as members of the team approached the mist nets holding these individuals, they quickly recognized them as *A. lituratus*. These bats were easily identified by several external characteristics, including yellowish coloration of the

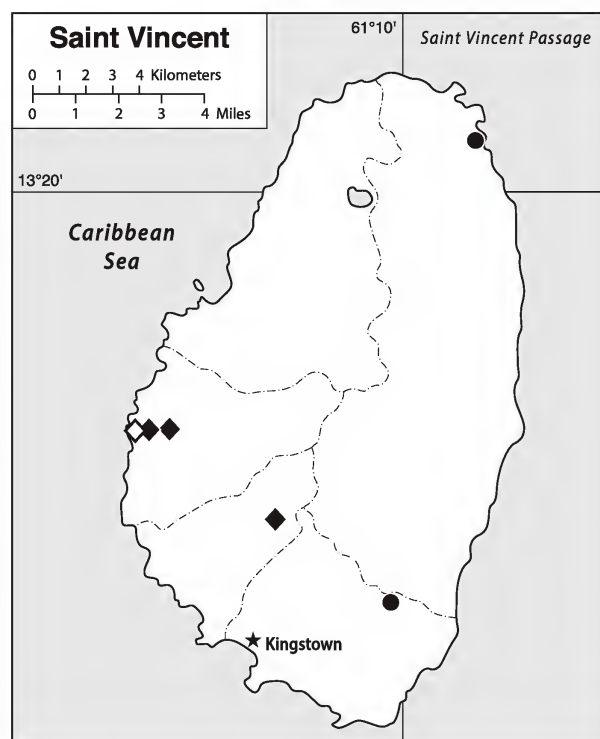


Figure 16. Map of the geographic distribution of *Artibeus lituratus* and *Tadarida brasiliensis* on the Lesser Antillean island of St. Vincent. Symbols represent: closed circles, specimens examined for *Artibeus lituratus*; closed diamonds, specimens examined for *Tadarida brasiliensis*; open diamond, literature record of *Tadarida brasiliensis*.

tragus and pinnae; very well defined, bright white facial stripes; a distinctive russet orangey-brown pelage; a larger more robust body; an obviously aggressive attitude when being handled.

There have been several phylogenetic analyses of *A. lituratus* (Phillips et al. 1991; Ditchfield 2000; Redondo et al. 2008; P. Larsen et al. 2013). P. Larsen et al. (2010) included one of the two St. Vincent specimens (TTU 105292) in their analysis of *A. schwartzi* and P. Larsen et al. (2013) examined the demographics of *A. lituratus* throughout the Neotropics. P. Larsen et al. (2013) hypothesized a time of origin of approximately 1.6 million years for *A. lituratus* and, collectively, the genetic data from the species indicate a recent and rapid dispersal throughout northern South America with colonization of the Caribbean from the south (Redondo et al. 2008; P. Larsen et al. 2013).

Although our sample of *A. lituratus* from St. Vincent was too small for any statistical analyses, Genoways et al. (2010) found that individuals of *A. lituratus* from the Grenadine Islands were significantly larger ($P \leq 0.05$) than *A. schwartzi* for five measurements (length of forearm, greatest length of skull, condylobasal length, zygomatic breadth, and mastoid breadth). No significant differences ($P \geq 0.05$) between the species were found in length of the maxillary toothrow and breadth across upper molars. Postorbital constriction was significantly larger in *A. schwartzi* than in *A. lituratus* ($P \leq 0.01$). We would expect similar results if more individuals of *A. lituratus* were available from St. Vincent.

Table 1 presents the length of forearm and seven cranial measurements for our male specimens from St. Vincent. Comparing these measurements with those of eight males from Grenada (Genoways et al. 1998), TTU 105292 falls above the range of the Grenada sample for greatest length of skull, condylobasal length, zygomatic breadth, mastoid breadth, and length of maxillary toothrow, whereas KU 110181 falls above the range of the Grenada sample for zygomatic breadth and postorbital constriction. Comparing these measurements with those of six males from the Grenadine Islands (Genoways et al. 2010), TTU 105292 fell above the range of the Grenadine Island sample only for length of maxillary toothrow and breadth across upper molars, whereas KU 110181 fell within the range of the Grenadine Islands sample, except for mastoid breadth, which was 0.1 mm below the range.

Because the St. Vincent population of *A. lituratus* was very similar to those on Grenada and the Grenadine Islands to which Genoways et al. (1998, 2010) assigned the trinomial *A. l. palmarum*, we use this trinomial here. This subspecies originally was described from Trinidad so its presence in the southern Lesser Antilles was not unexpected.

The site where the first specimen of this species was captured was along the ridge that forms the southern rim of the Mesopotamia Valley. This fertile valley, which lies just to the northeast of Kingstown, was under extensive agricultural development, dominated by bananas. Other fruits growing in the area that would be of value to bats include nutmeg, cocoa, breadfruit,

soursop, and coconuts. The nets on this evening were placed in an area where bananas and second growth brush predominated the habitat. In addition to the single *A. lituratus* taken on this evening, other species taken were *A. schwartzi*, *B. cavernarum*, *G. longirostris*, and *M. plethodon*.

The site at Old Sandy Bay was chosen in haste and because no better site had been located before darkness was ready to set in. The site was just across the Windward Highway from the beach and Atlantic Ocean. We set one net in a small, dry streambed filled with pioneer tropical vegetation and dominated by several coconut palm trees at one edge of the area. Our other two mist nets were placed across a rough road leading up a steep hill to an area of agricultural development. In a pasture at one side of the road was a small grove of oil palm trees. No bats were taken in the net across the dry streambed. One *A. lituratus* was taken in each of the nets across the road along with *G. longirostris* and *A. schwartzi*. Muñoz-Romo et al. (2008) suggested that this species day roosts in palm trees, which may account for their captures at our site.

The three specimens of *A. lituratus* captured on St. Vincent were males. The two individuals taken on 5 June 2006 had testes in a scrotal position and each had a testes length of 8.0. These males weighed 61.9 and 66.0.

***Artibeus schwartzi* J. K. Jones, Jr., 1978**
Schwartz's Fruit-eating Bat

Specimens examined (381).—**Charlotte Parish:** Colonarie River, 1 km S, 2.4 km W South Rivers, 248 m [13°14'10.4"N, 61°09'52.7"W], 4 (TTU 105633–36); Fancy River trap, 0.6 km S, 0.3 km E Fancy, 150 m [13°22'31.7"N, 61°08'56.1"W], 2 (TTU 105656–57); Golden Grove, 1.5 km N, 2.7 km W Mesopotamia, 410 m [13°13'58.3"N, 61°11'32.7"W], 6 (TTU 105323–26, 105328, 105330); 1.2 km N, 2 km W Greiggs, 445 m [13°13'18.2"N, 61°10'42.7"W], 12 (TTU 105298–309); La Soufriere Trail, 0.7 km N, 5.1 km W Orange Hill, 646 m [13°19'22.8"N, 61°10'01.2"W], 6 (TTU 105343–48); La Soufriere Trailhead, 3.7 km W Orange Hill, 420 m [13°19'00.2"N, 61°09'01.2"W], 6 (TTU 105368–73); Mesopotamia, 350 ft., 2 (KU 110176–77); 0.6 km S Mesopotamia, 15 (CM 83257–71); Montreal trap; 1.5

km N, 1.5 km W Richland Park, 473 m [13°12'30.7"N, 61°11'20.4"W], 4 (TTU 105665–68); 0.35 km N, 0.2 km W Old Sandy Bay, 57 m [13°21'41.4"N, 61°08'07.9"W], 2 (TTU 105294–95); Above Owia, 0.5 km S, 0.3 km W Owia, 172 m [13°22'10.7"N, 61°08'57.1"W], 3 (TTU 105383–85); Perseverance, 0.2 km N, 3.1 km W Georgetown, 250 m [13°16'38.7"N, 61°08'52.0"W], 7 (TTU 105408–14); 1 km S Peruvian Vale, 4 (CM 83203–06); Yambou River Gorge, W Peruvian Vale, 49 m [13°10'16.8"N, 61°09'14.8"W], 16 (TTU 105431–46). **St. Andrew Parish:** Buccament River, 5 (ROM 79104–06, 79108, 79111); Lower Buccament River, Buccament, 2 m [13°11'30.2"N, 61°00'16.6"W], 4 (TTU 105736–39); Mt. St. Andrew, 0.35 km S, 3.0 km E Pembroke, 501 m [13°11'12.6"N, 61°13'07.0"W], 7 (TTU 105480–86); Parrot Lookout, Vermont Nature Trail, 2.3 km N, 1.75 km E Vermont, 496 m [13°13'20.2"N, 61°12'43.4"W], 2 (TTU 105768–69); Trailhead for Vermont Nature Trail, 1.4 km N, 1.5 km E Vermont, 310 m [13°12'18.8"N, 61°12'53.4"W], 2 (TTU 105808–09); Vermont Nature Trail, 1.6 mi E Vermont (by road), 1 (NMNH 580671); Waterworks, 1.25 km N, 1.6 km E Vermont, 310 m [13°12'35.6"N, 61°12'52.0"W], 4 (TTU 105467–70). **St. David Parish:** Falls of Baleine, 13 km S, 2.6 km W Fancy, 130 m [13°22'13.6"N, 61°11'36.2"W], 10 (TTU 105512–21); Morgan Woods, 0.4 km N, 2.4 km E Richmond, 253 m [13°18'28.9"N, 61°12'27.9"W], 8 (TTU 105525–32); 0.3 km S, 2.2 km E Rose Hall, 435 m [13°15'58.3"N, 61°13'21.9"W], 2 (TTU 105488–89); 0.7 km S, 1.75 km E Rose Hall, 379 m [13°15'46.9"N, 61°13'35.4"W], 6 (TTU 105493–98); 0.75 km S, 2.3 km E Rose Hall, 377 m [13°15'51.2"N, 61°13'25.7"W], 2 (TTU 105504–05). **St. George Parish:** Botanical Garden, Liberty Lodge, 71 m [13°09'55.5"N, 61°13'40.8"W], 79 (77 TTU 105826–63, 105867–905; 2 ROM 74430, 74432); 1 km NE Brighton Village, 3 (UNSM 19265–67); 1.3 km N, 2.7 km E Calliagua, 50 (CM 83207–83256); Calliagua, 12 (AMNH 219159–69, 276696); Cane Garden Point Cave, Cane Garden, 2 m [13°08'24.3"N, 61°13'43.1"W], 1 (TTU 105913); Clifton Hill, 10 (KU 110178–80, 82–83, 110185–86, 110196–98); Dennis' Cave, Cane Garden, 2 m [13°08'16.9"N, 61°13'36.0"W], 2 (TTU 105914–15); Evesham, 155 m [13°10'10.7"N, 61°10'12.9"W], 6 (TTU 105918–23); E side Kings Hill, 1 (NMNH 580670); Kingstown, 150 ft., 7 (KU 110206–09, 110211–13); Milikin Bay, near Prospect, 10 m [13°07'59.3"N, 61°10'03.5"W],

2 (TTU 105942–43); Mount Pleasant Ruin, 104 m [13°09'02.9"N, 61°09'13.1"W], 10 (TTU 105928–37); Mt. St. Andrew, 1.75 km N, 0.3 km E Green Hill, 633 m [13°11'17.9"N, 61°12'56.8"W], 2 (TTU 105544–45); Ratho Mill, 11 (10 KU 112005, 151605–13; 1 NMNH 395029); Rose Cottage area, Villa Point, West Side, between Indian Bay and Greathead Bay, 21 (NMNH 580664–69, 580672–73, 580695–707). **St. Patrick Parish:** Convent, 0.4 km N, 3 km E Grove, 440 m [13°14'53.5"N, 61°12'32.1"W], 2 (TTU 105967–68); Mount Wynne Caves, Mount Wynne Bay, 0 m [13°13'03.6"N, 61°16'30.4"W], 1 (TTU 105980); Wallilabou, 10 m [13°14'54.2"N, 61°16'09.1"W], 2 (TTU 105983–84); Wallilabou Falls, 0.6 km E Wallilabou, 55 m [13°14'54.2"N, 61°15'37.7"W], 11 (TTU 105551–53, 105988–95); Wallilabou River Gorge, 0.1 km S, 1.8 km E Wallilabou, 170 m [13°14'31.7"N, 61°15'8.0"W], 6 (TTU 105567–72).

Additional records.—**St. George Parish:** Clifton Hill (Jones 1978); Kingstown (Jones 1978); Ratho Mill (Jones 1978; Timm and Genoways 2003). **No Specific Parish:** no specific locality (Andersen 1908; G. M. Allen 1911; Koopman 1968; Vaughan 1995; Vaughan and Hill 1996).

Specimens captured/released (690).—**Charlotte Parish:** Colonaire River, 1 km S, 2.4 km W South Rivers, 248 m [13°14'10.4"N, 61°09'52.7"W], 45; Fancy River trap, 0.6 km S, 0.3 km E Fancy, 150 m [13°22'31.7"N, 61°08'56.1"W], 17; Golden Grove, 1.5 km N, 2.7 km W Mesopotamia, 410 m [13°13'58.3"N, 61°11'32.7"W], 19; 1.2 km N, 2 km W Greiggs, 445 m [13°13'18.2"N, 61°10'42.7"W], 18; La Soufriere Trail, 0.7 km N, 5.1 km W Orange Hill, 646 m [13°19'22.8"N, 61°10'01.2"W], 4; La Soufriere Trailhead, 3.7 km W Orange Hill, 420 m [13°19'00.2"N, 61°09'01.2"W], 25; Montreal trap, 1.5 km N, 1.5 km W Richland Park, 473 m [13°12'30.7"N, 61°11'20.4"W], 45; 0.35 km N, 0.2 km W Old Sandy Bay, 57 m [13°21'41.4"N, 61°08'07.9"W], 15; Owia Big River Cave, 0.3 km S, 0.3 km W Owia, 97 m [13°22'15.1"N, 61°08'56.1"W], 1; Perseverance, 0.2 km N, 3.1 km W Georgetown, 250 m [13°16'38.7"N, 61°08'52.0"W], 17; Yambou River Gorge, W Peruvian Vale, 49 m [13°10'16.8"N, 61°09'14.8"W], 30. **St. Andrew Parish:** Lower Buccament River, Buccament, 2 m [13°11'30.2"N, 61°00'16.6"W], 34; Mt. St. Andrew, 0.35 km S, 3.0 km E Pembroke, 501 m

[13°11'12.6"N, 61°13'07.0"W], 29; Parrot Lookout, Vermont Nature Trail, 2.3 km N, 1.75 km E Vermont; 496 m [13°13'20.2"N, 61°12'43.4"W], 40; Trailhead for Vermont Nature Trail, 1.4 km N, 1.5 km E Vermont, 310 m [13°12'18.8"N, 61°12'53.4"W], 23; Waterworks, 1.25 km N, 1.6 km E Vermont, 310 m [13°12'35.6"N, 61°12'52.0"W], 12. **St. David Parish:** Falls of Baleine, 13 km S, 2.6 km W Fancy, 130 m [13°22'13.6"N, 61°11'36.2"W], 2; Morgan Woods, 0.4 km N, 2.4 km E Richmond, 253 m [13°18'28.9"N, 61°12'27.9"W], 24; 0.3 km S, 2.2 km E Rose Hall, 435 m [13°15'58.3"N, 61°13'21.9"W], 5; 0.7 km S, 1.75 km E Rose Hall, 379 m [13°15'46.9"N, 61°13'35.4"W], 2; 0.75 km S, 2.3 km E Rose Hall, 377 m [13°15'51.2"N, 61°13'25.7"W], 5. **St. George Parish:** Botanical Garden, Liberty Lodge, 71 m [13°09'55.5"N, 61°13'40.8"W], 64; Evesham, 155 m [13°10'10.7"N, 61°10'12.9"W], 11; Milikin Bay, near Prospect, 10 m [13°07'59.3"N, 61°10'03.5"W], 12; Mount Pleasant Ruin, 104 m [13°09'02.9"N, 61°09'13.1"W], 1; Mt. St. Andrew, 1.75 km N, 0.3 km E Green Hill, 633 m [13°11'17.9"N, 61°12'56.8"W], 11. **St. Patrick Parish:** Convent, 0.4 km N, 3 km E Grove, 440 m [13°14'53.5"N, 61°12'32.1"W], 17; Wallilabou, 10 m [13°14'54.2"N, 61°16'09.1"W], 20; Wallilabou Falls, 0.6 km E Wallilabou, 55 m [13°14'54.2"N, 61°15'37.7"W], 121; Wallilabou River Gorge, 0.1 km S, 1.8 km E Wallilabou, 170 m [13°14'31.7"N, 61°15'8.0"W], 21.

The evolutionary history of *Artibeus schwartzi* (*sensu* P. Larsen et al. 2007) has long fascinated Caribbean bat biologists, and multiple hypotheses regarding the origin of the species have been proposed (Pumo et al. 1988, 1996; Jones 1989; Phillips et al. 1989, 1991; P. Larsen et al. 2010). Thus, the account of *A. schwartzi* spans decades of research and it was one of the most fascinating aspects of the bats of St. Vincent, as it provides a greater understanding of the dynamism of the evolutionary forces that have shaped species diversity observed across insular systems. We provide a detailed account of the taxonomic and evolutionary history of *A. schwartzi* here.

Historically identified as *A. jamaicensis*, the large body size of *A. schwartzi* contributed to much debate regarding the appropriate taxonomic classification of the species (Hershkovitz 1949; Koopman 1968; Jones 1978; P. Larsen et al. 2007, 2010). Owing to its size, the bat was frequently misidentified as *A. lituratus*;

however, Jones (1978) provided diagnostic characters uniting St. Vincent specimens with *A. jamaicensis* and formally applied the trinomial *A. jamaicensis schwartzi*. Until the early 1990's, hypotheses regarding the evolutionary history of *schwartzi* were based almost entirely on morphological data as compared to specimens of *Artibeus* collected from islands to the north and south of St. Vincent (Andersen 1908; Koopman 1968; Jones and Phillips 1970). A remarkable pattern emerged from these studies, as they suggested the contemporary population of *schwartzi* resided at the center of at least two separate Caribbean invasions of *Artibeus* that converged on St. Vincent from both northern and southern colonization routes. It was hypothesized that *A. jamaicensis jamaicensis* colonized the northern Lesser Antilles from the west, having originated from Central America and the Greater Antilles, expanding southward throughout the Lesser Antilles, south to St. Vincent. The second invader, *A. jamaicensis trinitatus*, invaded the Caribbean from northern South America, colonizing Trinidad and Tobago, northward to St. Vincent. This fascinating observation led Jones (1989) to hypothesize that the large size of *schwartzi* was "...a classic case of heterosis resulting from hybridization between the two invading groups."

It was the advent of molecular systematics in the 1990's that provided an incredible insight with respect to the hypothesis of hybridization and heterosis involving *schwartzi*. A series of publications utilized restriction site mapping of mitochondrial DNA (mtDNA) to investigate genetic variation across the putative hybrid-zone (St. Lucia south to Trinidad, including Barbados) (Pumo et al. 1988, 1996; Phillips et al. 1989, 1991). These studies confirmed the hypothesis of dual invasion routes by *Artibeus* as well as hybridization across the southern Lesser Antilles (Pumo et al. 1996). Most striking however, was the discovery that the St. Vincent population of *schwartzi* exhibited mtDNA variation that was distinct from both invading lineages. This observation led Phillips et al. (1989) to hypothesize that the St. Vincent population of *schwartzi* was "...derived from a stock that reached the Antilles earlier than others and this could explain the evolution of the morphological distinctive *A. j. schwartzi*."

The hypothesis of hybridization among three subspecies of *A. jamaicensis* was perhaps unremarkable when considered within the greater context of

natural mammalian hybrid-zones between geographically defined subspecies (Hewitt 1988). However, this hypothesis was formulated in the absence of a genetic perspective of the variation across the genus *Artibeus* as well as within the *A. jamaicensis* complex (13 subspecies *sensu* Simmons 2005). P. Larsen et al. (2007) performed phylogenetic analyses on cytochrome-*b* DNA sequence data from an expansive sampling of 176 individuals, collectively representing all 13 subspecies within the *A. jamaicensis* complex, including the nominate *A. j. jamaicensis* from Jamaica. Importantly, their analyses provided statistical support for species-level classification of *A. schwartzi* and *A. planirostris* (from Trinidad). Moreover, P. Larsen et al. (2007) formally assigned the subspecific taxon *trinitatus* to *A. planirostris*. Thus, in the context of species-level variation within *Artibeus*, the Lesser Antillean hybrid-zone involved three putative species-level lineages: *A. jamaicensis*, *A. schwartzi*, and *A. planirostris*.

The first genome-wide molecular characterization of *A. schwartzi* was performed by P. Larsen et al. (2010). They used nuclear Amplified Fragment Length Polymorphisms (AFLPs), in combination with morphometric and mitochondrial DNA sequence datasets, to measure the genetic and morphological variation across the Lesser Antillean *Artibeus* hybrid-zone. The results of P. Larsen et al. (2010) provided additional support for the hypothesis of hybridization among *Artibeus* species in the southern Lesser Antilles and indicated that the nuclear genome of *A. schwartzi* on St. Vincent was a product of admixture between *A. jamaicensis* (invading St. Vincent from the north) and *A. planirostris* (invading St. Vincent from the south). Moreover, their morphometric data revealed substantial phenotypic diversity within *A. schwartzi* and identified morphological patterns consistent with hybrid-induced morphological phenotypes (P. Larsen et al. 2010). These results, in combination with previous work by Pumo et al. (1988, 1996) and Phillips et al. (1989, 1991) provide robust support for the presence of a dynamic hybrid-zone, centered on St. Vincent, that involved three species of *Artibeus*.

It is likely that the distinct mitochondrial genome of *A. schwartzi* originated from a South American ancestor that colonized the southern Lesser Antilles before either *A. jamaicensis* or *A. planirostris*, perhaps

during the Pleistocene. Support for this hypothesis was found in the genetic variation observed across mtDNA sequence datasets and the documentation of a mtDNA haplotype closely related to *A. schwartzi* in northern Venezuela (P. Larsen et al. 2007, 2010). Subsequent Caribbean invasions of *A. jamaicensis* and *A. planirostris* during the Holocene likely contributed to local extinction events of *A. schwartzi* throughout the Lesser Antilles, with the St. Vincent population representing the very center of an ongoing hybrid swarm that formed within the last 30,000 years (P. Larsen et al. 2010). The lack of structure observed in nuclear genome AFLPs, in combination with the distinct mtDNA haplotype and morphological phenotype of *A. schwartzi*, led P. Larsen et al. (2010) to hypothesize that the extant St. Vincent population of *A. schwartzi* represents a fascinating case of reticulate evolution that was facilitated by a combination of incomplete reproductive isolating mechanisms among recently evolved lineages of *Artibeus* and ecologically limited insular habitats in the southern Lesser Antilles. Recent advancements in population genomics are contributing to the discovery of reticulated evolutionary histories of a number of taxa and it is likely that the formation of hybrid evolutionary trajectories is linked with classical island biogeography (P. Larsen et al. 2010; Twyford and Ennos 2012; Amaral et al. 2014; Grant and Grant 2014, 2015; Kuo et al. 2015). Indeed, a strikingly similar example to that of *A. schwartzi* was found on the Galapagos island of Daphne Major, where introgressive hybridization between *Geospiza fortis* and *G. scandens* finches was hypothesized to have culminated in the formation of a unique species-level evolutionary trajectory (Grant and Grant 2014). The finch data from Daphne Major indicates that ecological forces operating on young closely-related taxa that are distributed across relatively small and restricted insular environments can facilitate introgressive hybridization and, at the same time, provide a mechanism for the isolation of hybrids from parental taxa. Thus, traditional aspects of island biogeography may provide ideal conditions for reticulate evolution as hypothesized by P. Larsen et al. (2010) and documented by Grant and Grant (2014).

Table 1 presents the length of forearm and seven cranial measurements of 21 adult male and 31 adult female *A. schwartzi*. No measurement revealed significant secondary sexual variation. Males averaged larger

than females for five cranial measurements including greatest length of skull, zygomatic breadth, mastoid breadth, length of maxillary toothrow, and breadth across the upper molars. The sexes averaged the same for condylobasal length.

Vaughan Jennings et al. (2004) found the echolocation calls of *A. schwartzi* from St. Vincent were frequency modulated, of very low intensity, and contained at least five harmonics, with the most intensity in the second or third harmonic. They also found that these bats had wings with average aspect ratios, low wing tip index, and extremely high wing loading. Vaughan Jennings et al. (2004) concluded that this combination of characters allowed *A. schwartzi* to fly slowly in cluttered space, with good turning ability.

Schwartz's Fruit-eating Bat was the most abundant species captured (47% of total captures) on St. Vincent in an ecological survey conducted in 1994 by Vaughan and Hill (1996). This bat was also the most abundant bat caught during our work in 2005–2006—47.1% (926/1968) of total captures. We netted this species at all of our net sites and found it at four roost sites—two caves and two ruins (Fig. 17).

One of our major collecting sites for these fruit-eating bats was the Botanical Garden in the Liberty Lodge section of Kingstown (Fig. 18). This was one of the oldest botanical gardens in the Western Hemisphere, being founded in 1765 with both a display and economic mission. It covers nearly 8 ha, with a variety of buildings, manicured lawns, and a collection of exotic and Caribbean native flowers and trees. The central gardens are dominated by mature palm trees of several species. Among the economically valuable exotic plants was a third generation breadfruit tree, a sucker from the original plant brought by Captain William Bligh (of *Bounty* fame) from his second voyage to Tahiti in 1793. Other trees in the garden that would be of value to bats include mango, soursop, papaya, trumpet tree, wild nutmeg, fiddlewood, and teak. We placed 10 nets throughout the grounds of the garden under and between the larger trees. One hundred and forty-one specimens of *A. schwartzi* were captured by 2200 hrs along with individuals of *G. longirostris* and *M. molossus*.

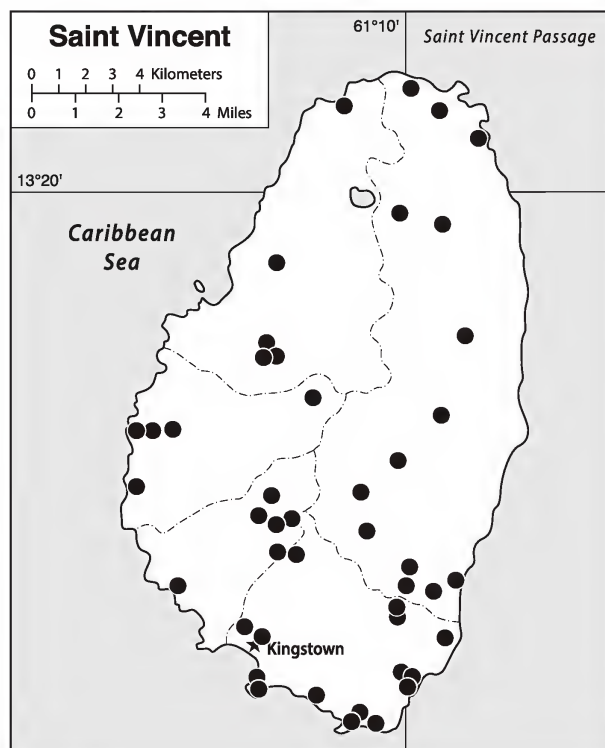


Figure 17. Map of the geographic distribution of *Artibeus schwartzi* on the Lesser Antillean island of St. Vincent. Closed circles represent specimens examined.

The collecting site near Evesham was located on the southern slopes of the Mesopotamian Valley, which was dominated by banana plantations. There also were scattered coconut palms and small patches of secondary native plants in non-cultivated areas. Mist nets were placed within the banana groves and across access roads through the plantations where we netted 17 individuals of *A. schwartzi*, 12 *G. longirostris*, and two *M. molossus*.

The field site at the Falls of Baleine was actually located on a semi-level area on the steep hill above the Falls. The trail leading above the Falls was steep, muddy, and grown up in waist- to shoulder-high grass. Five nets were placed in this level area under and around mango trees, cocoa trees, wild red gingers, and bushes of pepper plant. Bat activity was very slow, resulting in the capture of only 14 individuals—*A. schwartzi* (12), *G. longirostris* (1), and *S. paulsoni* (1).



Figure 18. Photograph of the Botanical Garden, Liberty Lodge, St. George Parish, St. Vincent. This is the oldest Botanical Garden established in the Western Hemisphere in 1765. The large tree in the center of the photograph is a breadfruit tree derived from a sucker from the original plant brought to St. Vincent by Captain William Bligh (of *Bounty* fame) from his second voyage to Tahiti in 1793. One hundred and forty-one individuals of *Artibeus schwartzi* were captured in the botanical garden on one evening before 2200 hrs.

The Mount Pleasant Ruin was the concrete shell of an uncompleted resort destroyed by a hurricane. We used hand nets to capture 11 *A. schwartzi* and five *G. longirostris* as they flew through corridors and side rooms. They seemed to settle in the dark recesses of what were designed to be closet spaces in each room, but these two species displayed more light tolerance in their day roosts than other species on the island.

Cane Garden Point Cave was primarily an erosion pocket in the same bluff of volcanic rock as Dennis' Cave located just to the southeast. Passing nearly 20

m into the bluff, this fissure-like space measured approximately 6 to 7 m in height and 2 to 3 m in width at the entrance. We caught *A. schwartzi* in holes in the ceiling near the entrance using hand nets attached to long poles. There were no bats in the shallow, tapering back part of the cave. Cave occupancy was low presumably because of its exposure to light and its location being subjected to storm surges. Like its close relative *A. jamaicensis*, *A. schwartzi* often selects roosts in well-illuminated areas (Genoways et al. 2005).

Currently, data on reproduction in *A. schwartzi* are limited making this information from St. Vincent of particular importance. A female captured on 18 May 1977 carried a single embryo measuring 10 in crown-rump length, whereas a male from earlier in the month (7 May 1977) was not reproductively active. A total of 228 females of *A. schwartzi* were examined from St. Vincent from the period of late May to early June at the end of the dry season and the beginning of the wet season. Of these females, 56 were pregnant and another 26 individuals were pregnant and lactating. Fifteen embryos from the former group had a mean crown-rump length of 21.2 (6.0–48.0), which was closely matched by the mean crown-rump length of the latter group of 21.6 (5.0–35.0). Among the remaining females, 57 were lactating, 12 were post-lactating, 53 evinced no gross reproductive activity, and 24 were volant young with unfused phalangeal epiphyses. Two hundred and eleven male bats were examined during this same period of which 142 had testes in a scrotal position, 49 had testes in non-scrotal position, and 20 were volant young with unfused phalangeal epiphyses. Ten of the scrotal males had a mean testes length of 8.1 (6.0–10.0), whereas 10 of the non-scrotal males had mean testes lengths of 4.9 (3.0–7.0). On 13–14 July 1970, two females were captured that were judged to be both pregnant and post-lactating, whereas two males had testes in a scrotal position and three had testes in an inguinal position. We examined 230 females of *A. schwartzi* from the height of the rainy season at the end of July and early August. This group of females remained reproductively active, but there were indications this reproductive cycle was closing. The most common reproductive state at this point in time was the exhibition of no gross reproductive activity represented by 101 females. Sixty-four of the remaining females presented as lactating, 35 were post-lactating, 28 car-

ried a single embryo, and two were volant young bats with unfused phalangeal epiphyses. It was noteworthy that none of the females were judged to be lactating and pregnant. Three of the pregnant females carried embryos that measured 40, 42, and 48 in crown-rump length. Among 254 male bats examined from this time, 185 had testes in a scrotal position, 65 had testes in an inguinal position, two were volant young with unfused phalangeal epiphyses, and two were non-volant young. The mean testes length of 10 of the scrotal males was 8.6 (5.0–11.0), whereas the mean testes length of 10 non-scrotal males was 3.7 (3.0–5.0). Four females captured 22–24 August 1967 revealed no reproductive activity. Eleven males taken on these dates had an average length of testes of 9.0 (4.0–12.0). Two females taken on 28 December 1961 appeared to be reproductively inactive.

These reproductive data do resemble those of the closely related species *A. jamaicensis*, which was considered to follow a bimodal polyestry cycle (Wilson 1979). Parturition in this reproductive cycle occurs at the end of the dry season from April into June, with a second burst of parturition in late July and August. With both pregnant females and pregnant and lactating females present on St. Vincent during the early June study period, at least some of the females appear to be undergoing a postpartum estrus, which leads to the second peak in births in late July and early August. Our meager data for late August and later in the calendar year suggest that there was no postpartum estrus following the July–August births and that no reproductive activity occurred as the wet season was closing.

At the end of the dry season and the beginning of the wet season, female body mass data were as follows: 15 reproductively inactive, 54.4 (44.4–62.3); 30 lactating, 59.3 (49.2–72.2); five post-lactating, 56.6 (46.0–64.3); 18 pregnant and lactating, 64.4 (53.1–72.2); 19 pregnant, 64.6 (48.7–79.7); and 21 volant young of the year, 48.7 (43.0–55.4). Data for males during this same time period were as follows: 85 sexually active (testes scrotal), 55.0 (44.8–65.8); 22 sexually inactive (testes inguinal), 51.5 (42.8–64.8); 18 volant young of the year, 49.7 (43.8–54.2); and two non-volant young, 22.7, 31.2. At the height of the wet season in late July and early August, female *A. schwartzi* had the following mean body masses: 13 reproductively inactive, 54.2

(43.6–65.5); seven lactating, 51.8 (41.2–63.5); five post-lactating, 51.3 (44.2–64.3); and three pregnant, 59.8, 73.5, 77.6. During this same time period, male body mass was as follows: 20 sexually active (testes scrotal), 52.2 (42.2–66.8); six sexually inactive (testes inguinal), 51.7 (49.9–54.7); and three non-volant young, 12.3, 28.2, 36.7.

Genoways et al. (2010) reviewed data concerning variation in the presence/absence of the upper M3 and lower m3 in Antillean populations of the *Artibeus jamaicensis* complex. They concluded that the presence/absence of the upper M3 was a species-level character, whereas presence/absence of the lower m3 in this *Artibeus* complex was neither an indication of geographic variation nor a species-level character, but rather a low occurrence polymorphism. We examined 36 individuals of *A. schwartzi* from St. Vincent, finding 32 lacking the upper M3 and four possessing them, giving a percent occurrence of 11.6%, which compares closely with 12.9% reported by Genoways et al. (2010) for 31 members of the island's population. Even at these relatively low rates of occurrence the hybrid nature of *A. schwartzi* was supported by these findings (P. Larsen et al. 2007, 2010). Populations of *Artibeus* from the Bahamas, Greater Antilles, and south at least as far as Dominica in the Lesser Antilles, to which we would now apply the name *A. jamaicensis*, uniformly lacked the upper third molars. Populations on Trinidad considered to be *A. planirostris* had 100% of the individuals examined have the upper M3 present. In the Grenada population, 89% of the individuals have the upper M3 indicating a strong relationship with *A. planirostris*, but also suggesting some genetic introgression from *A. jamaicensis*. Further north in the Grenadine Islands the overall rate of occurrence of the upper M3 was only 3.6%, but the rate of occurrence of the upper M3 was higher again on St. Vincent (11.6%), thus associating a low rate of presence of the upper M3 with *A. schwartzi*. We also examined these 36 individuals for the occurrence of the lower m3, but this polymorphism does not occur in these individuals as all have these teeth present. This was the same result obtained by Genoways et al. (2010) based on 21 specimens from St. Vincent.

A male from 1.3 km N and 2.7 km E of Calliagua (CM 83,242) was missing the first and second lower left

incisors and the first lower right incisor. The alveolus of the upper right canine and first premolar was thin and pitted. The upper left canine was darkened, possibly as the result of an infection.

***Ardops nichollsi vincentensis* R. Larsen, Genoways, and Baker, 2017**
Antillean Tree Bat

Specimens examined (36).—**Charlotte Parish:** Colonarie River, 1 km S, 2.4 km W South Rivers, 248 m [13°14'10.4"N, 61°09'52.7"W], 5 (TTU 105628–32); Fancy River trap, 0.6 km S, 0.3 km E Fancy, 150 m [13°22'31.7"N, 61°08'56.1"W], 1 (TTU 105655); Golden Grove, 1.5 km N, 2.7 km W Mesopotamia, 410 m [13°13'58.3"N, 61°11'32.7"W], 7 (TTU 105316–22); La Soufriere Trail, 0.7 km N, 5.1 km W Orange Hill, 646 m [13°19'22.8"N, 61°10'01.2"W], 1 (TTU 105342); La Soufriere Trailhead, 3.7 km W Orange Hill, 420 m [13°19'00.2"N, 61°09'01.2"W], 3 (TTU 105365–67); Montreal trap, 1.5 km N, 1.5 km W Richland Park, 473 m [13°12'30.7"N, 61°11'20.4"W], 1 (TTU 105664). **St. Andrew Parish:** Mt. St. Andrew, 0.35 km S, 3.0 km E Pembroke, 501 m [13°11'12.6"N, 61°13'07.0"W], 1 (TTU 105479); Parrot Lookout, Vermont Nature Trail, 2.3 km N, 1.75 km E Vermont, 496 m [13°13'20.2"N, 61°12'43.4"W], 10 (TTU 105758–67); Vermont Nature Trail, 1.6 mi E Vermont (by road), 5 (NMNH 580676, 580710–13). **St. David Parish:** Morgan Woods, 0.4 km N, 2.4 km E Richmond, 253 m [13°18'28.9"N, 61°12'27.9"W], 1 (TTU 105524). **St. George Parish:** E side Kings Hill, 1 (NMNH 580675).

Additional records.—**No Specific Parish:** no specific locality (Jones and Schwartz 1967; Koopman 1968; Vaughan 1995; Vaughan and Hill 1996).

Specimens captured/released (12).—**Charlotte Parish:** Fancy River trap, 0.6 km S, 0.3 km E Fancy, 150 m [13°22'31.7"N, 61°08'56.1"W], 1; Golden Grove, 1.5 km N, 2.7 km W Mesopotamia, 410 m [13°13'58.3"N, 61°11'32.7"W], 11.

The genus *Ardops* was diagnosed and named by Miller (1906) based on three species, *Stenoderma nichollsi* Thomas (type species) from Dominica, *S. montserratensis* Thomas from Montserrat, and *S. luciae* Miller from St. Lucia, and subsequently Miller

(1913a) named a fourth species, *Ardops annectens* from Guadeloupe. The stenodermine bat genus *Ardops*, endemic to the Lesser Antilles, is related to three other endemic Antillean genera, *Ariteus* of Jamaica, *Phyllops* of Cuba and Hispaniola, and *Stenoderma* of Puerto Rico and the Virgin Islands. These four Antillean endemic genera were all placed in the genus *Stenoderma* by Varona (1974), but all subsequent authors referred to these as distinct genera. *Ardops* and *Ariteus* are sister genera and are basal to *Stenoderma* in a concatenated mitochondrial and nuclear gene phylogeny based on Baker et al. (2003). These genera share a most recent common ancestor approximately 5.42 mya (6.2–4.6; Baker et al. 2012). In two recent studies (Baker et al. 2016; Cirranello et al. 2016), the four Antillean genera (*Ardops*, *Ariteus*, *Phyllops*, and *Stenoderma*) were placed in the subtribe Stenodermatina along with four mainland genera indicating a close relationship in this diverse radiation that geographically spans Mexico, Central and South America, and the Caribbean regions. This group was characterized by a shortened face or rostrum, white shoulder spots, and a suite of molecular characters.

Four species of *Ardops* were recognized prior to the taxonomic revision by Jones and Schwartz (1967), who recognized these taxa as subspecies and described one additional subspecies. Subsequently, R. Larsen et al. (2017), in a molecular and morphological analysis, described a subspecies from St. Vincent and placed *A. n. annectans* as a synonym of *A. n. montserratensis*. The analysis of *Ardops* (R. Larsen et al. 2017) identified a consistent division between northern and southern island *Ardops* groups based on multiple molecular markers (cytochrome-*b*, AFLPs, and intronic zinc-finger Y-chromosome gene sequence). These markers allowed R. Larsen et al. (2017) to provide evidence of separate subspecies on St. Vincent and St. Lucia (*A. n. luciae* was once assigned to both islands). In their study, intraspecific variation of the cytochrome-*b* gene of *A. nichollsi* was low (< 1%), however, specimens collected from St. Vincent had unique cytochrome-*b* haplotypes from all other *A. nichollsi*. Additionally, there was statistical support in the cytochrome-*b* phylogeny for a sister relationship between St. Vincent and St. Lucia populations. AFLP data also supported a division between the St. Vincent and St. Lucia *Ardops* island clades (R. Larsen et al. 2017). Morphologically,

specimens from St. Vincent had significantly smaller cranial measurements than those from St. Lucia, and were more similar in size to specimens from Dominica. Together these findings provided strong support for the subspecies *luciae* on St. Lucia, but may also be indicative of more complex processes at play within this taxon, including incipient speciation, hybridization, and/or differing levels of lineage sorting (Funk and Omland 2003; Coyne and Orr 2004; McGuire et al. 2007; Yannic et al. 2008; P. Larsen et al. 2010). Minimally, the data from *Ardops* indicate a period of geographic isolation, corresponding to the Pleistocene (Rojas et al. 2011; Baker et al. 2012), where the appearance of island banks would have contributed to gene flow among populations of *A. nichollsi* in the northern Lesser Antilles (St. Eustatius, St. Kitts and Nevis, Antigua, Montserrat), but would have allowed for genetic isolation in populations distributed in the southern Lesser Antilles (St. Lucia and St. Vincent).

Based on data from these molecular and morphological analyses, the St. Vincent *Ardops nichollsi* population represents a distinct subspecies from *A. n. luciae* and was recognized as *A. n. vincentensis* (Fig. 19). Therefore, the monotypic genus *Ardops* is comprised of five subspecies: *A. n. montserratensis*—Montserrat (Pedersen et al. 1996, 2009), Nevis (Pedersen et al. 2003), St. Eustatius (Jones and Schwartz 1967), St. Kitts (Pedersen et al. 2005), St. Martin (Genoways et al. 2007b), Saba (Genoways et al. 2007a), Antigua (Lindsay et al. 2010), Guadeloupe (Baker et al. 1978), and Marie Galante (McCarthy and Henderson 1992); *A. n. nichollsi*—Dominica (Genoways et al. 2001); *A. n. koopmani*—Martinique (Jones and Schwartz 1967); *A. n. luciae*—St. Lucia (Pedersen et al. in press); and *A. n. vincentensis*—St. Vincent (R. Larsen et al. 2017).

Table 1 provides the length of forearm and seven cranial measurements from 13 male and 12 female *A. n. vincentensis* from St. Vincent. Females were significantly larger than males for all measurements, with $P \leq 0.001$ level for all measurements except length of forearm ($P \leq 0.01$) and postorbital constriction ($P \leq 0.05$).

Golden Grove was located on the eastern slope of Grand Bonhomme mountain high above the Mesopotamia Valley and was one of the highest elevations (410 m) from which we sampled on St. Vincent. Two

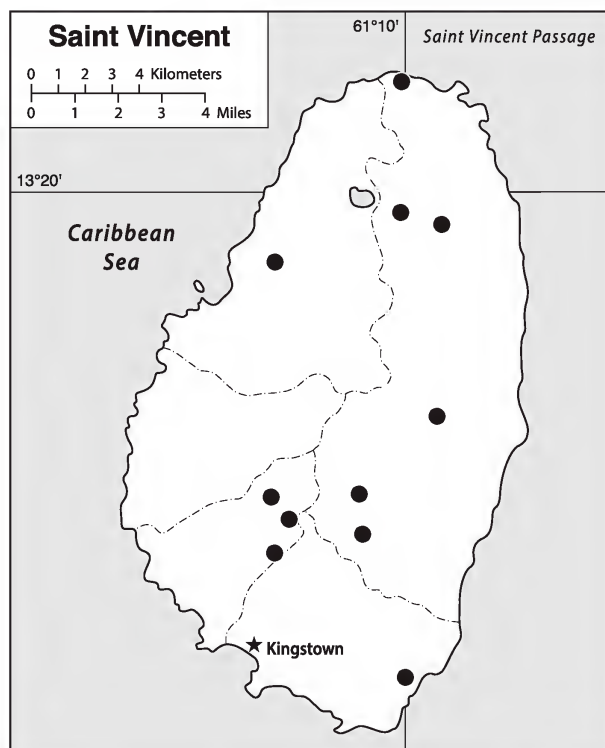


Figure 19. Map of the geographic distribution of *Ardops nichollsi* on the Lesser Antillean island of St. Vincent. Closed circles represent specimens examined.

general areas were netted at this location, with the first high on a flat area where two nets were set across the road and three nets were set down the slope in the forest adjacent to a variety of fruiting trees: banana, nutmeg, figs, breadfruit, and pepper plant. The dominant vegetation in the area included helecho gigante, santinay, ground ferns, tree fern, and bamboo. The first bat was seen flying at 1845 hr. We captured 18 *A. nichollsi* on this single night, which was the largest number taken anywhere on St. Vincent. Most were caught in the lowest shelf of the nets indicating that they were flying close to the ground. Five other species of bats were taken on this evening, including *G. longirostris*, *M. plethodon*, *A. schwartzi*, *S. paulsoni*, and *M. molossus*.

The road going to the La Soufriere trailhead travels up the picturesque windward coast and up the eastern slope of the volcano. It ends at a large picnic ground and parking lot at 125 m, just above where ag-

gricultural land gives way to the secondary rain forest. The trail continues up steep volcanic ridges verdant with bamboo and flowering trees before topping the crater rim. La Soufriere volcano rises to 1,234 m and is one of the most active volcanoes in the Western Hemisphere, with the most recent eruption in 1979. The volcano's slopes are covered with secondary rain forest because repeated eruptions have either destroyed or prevented primary forest. We placed four nets around the periphery of the parking lot, taking advantage of fruiting trees and obvious flyways through the secondary forest. Eight nets were also placed along the trail at 646 m as described in the account of *P. fuscus* above. Four *A. nichollsi* were netted, three at the trailhead and one near the tree line along the trail. Similar species were netted at these two very different locations (*P. fuscus*, *G. longirostris*, *M. plethodon*, *A. schwartzi*, and *S. paulsoni*) with the addition of *M. molossus* at the trailhead and *M. buriri* high up the trail.

On St. Vincent, the wet season begins in late May to early June. During this time, six of 16 females were observed to be lactating, five revealed no gross reproductive activity, one female was pregnant, and four were both lactating and pregnant, with three of these embryos measuring 8, 9, and 11 in crown-rump length. Of six males from this period, two had testes in a scrotal position with testes lengths of 4.0 and 4.5, whereas four had testes in an inguinal position of which two had testes lengths of 3.0 and 5.0. Of 15 females captured during the height of the rainy season (late July and early August), five were pregnant, with four of the embryos measuring 7, 23, 25, and 26 in crown-rump length, one was post-lactating, and seven were reproductively inactive. Two females and three males from this period were judged to be immature because the phalangeal epiphyses were not fused. Four adult males all had testes in a scrotal position, with a mean length of testes of 5.6 (4.0–8.5) and a juvenile male had testes measuring 2.5 in length. Pedersen et al. (2005) found that the population of *Ardops* exhibits bimodal polyestry on St. Kitts, producing young between March–April and June–July. *Ardops* on St. Vincent also exhibit bimodal polyestry involving a postpartum estrus, but the timing was much later with parturition occurring in May and then in August.

In late May and early June, seven adult males had an average weight of 13.0 (11.8–14.6), whereas five

non-reproductive females averaged 18.5 (17.7–19.4), six lactating females had a mean weight of 17.3 (14.9–20.4), four females that were lactating and pregnant had a mean weight of 17.2 (15.1–19.1), and one pregnant female weighed 16.4. In late July and early August, four adult males had a mean weight of 14.0 (13.1–14.8), whereas three reproductively inactive females had weights of 17.4, 17.4, and 19.6, two pregnant females weighed 17.5 and 19.5, and a post-lactating female weighed 19.7.

Family Molossidae

Molossus molossus molossus (Pallas, 1766)

Pallas' Mastiff Bat

Specimens examined (58).—**Charlotte Parish:** Colonarie River, 1 km S, 2.4 km W South Rivers, 248 m [13°14'10.4"N, 61°09'52.7"W], 6 (TTU 105644–49); Golden Grove, 1.5 km N, 2.7 km W Mesopotamia, 410 m [13°13'58.3"N, 61°11'32.7"W], 1 (TTU 105335); La Soufriere Trailhead, 3.7 km W Orange Hill, 420 m [13°19'00.2"N, 61°09'01.2"W], 1 (TTU 105376); Perseverance, 0.2 km N, 3.1 km W Georgetown, 250 m [13°16'38.7"N, 61°08'52.0"W], 2 (TTU 105417–18); Yambou River Gorge, W Peruvian Vale, 49 m [13°10'16.8"N, 61°09'14.8"W], 2 (TTU 105451–52). **St. Andrew Parish:** Buccament River, 1 (ROM 79092); Lower Buccament River, Buccament, 2 m [13°11'30.2"N, 61°00'16.6"W], 2 (TTU 105742–43); Mt. St. Andrew, 0.35 km S, 3.0 km E Pembroke, 501 m [13°11'12.6"N, 61°13'07.0"W], 3 (TTU 109110–12); Waterworks, 1.25 km N, 1.6 km E Vermont, 310 m [13°12'35.6"N, 61°12'52.0"W], 2 (TTU 105474–75). **St. George Parish:** Botanical Garden, Liberty Lodge, 71 m [13°09'55.5"N, 61°13'40.8"W], 5 (1 ROM 74465; 4 TTU 105909–12); 1 km NE Brighton Village, 1 (UNSM 19280); house NW Brighton Village, 5 (ROM 79069–70, 79074, 79076–77); 1.3 km N, 2.7 km E Calligua, 1 (CM 83425); Evesham, 155 m [13°10'10.7"N, 61°10'12.9"W], 2 (TTU 105926–27); Milikin Bay, near Prospect, 10 m [13°07'59.3"N, 61°10'03.5"W], 18 (TTU 105946–54, 105958–66); Ratho Mill, 2 (KU 152115–16). **St. Patrick Parish:** Convent, 0.4 km N, 3 km E Grove, 440 m [13°14'53.5"N, 61°12'32.1"W], 1 (TTU 105973); Wallilabou Falls, 0.6 km E Wallilabou, 55 m [13°14'54.2"N, 61°15'37.7"W], 3 (TTU 105556–57, 105998).

Additional records.—**St. George Parish:** Ratho Mill (Timm and Genoways 2003). **St. Patrick Parish:** Allen (1908, 1911) reports specimens as *Molossus crassicaudatus* but does not give a specific locality for the specimens; however, examining the original Museum of Comparative Zoology, Harvard University, catalog online indicates they came from Barrouallie.

Specimens captured/released (138).—**Charlotte Parish:** La Soufriere Trailhead, 3.7 km W Orange Hill, 420 m [13°19'00.2"N, 61°09'01.2"W], 4; Perseverance, 0.2 km N, 3.1 km W Georgetown, 250 m [13°16'38.7"N, 61°08'52.0"W], 70. **St. Andrew Parish:** Lower Buccament River, Buccament, 2 m [13°11'30.2"N, 61°00'16.6"W], 11; Waterworks, 1.25 km N, 1.6 km E Vermont, 310 m [13°12'35.6"N, 61°12'52.0"W], 4. **St. George Parish:** Milikin Bay, near Prospect, 10 m [13°07'59.3"N, 61°10'03.5"W], 32. **St. Patrick Parish:** Wallilabou Falls, 0.6 km E Wallilabou, 55 m [13°14'54.2"N, 61°15'37.7"W], 17.

This common “house bat” is a wide spread Neotropical species, occurring on most of the islands in the West Indies except the Bahamas. On the mainland the species occurs from northern Mexico through Central America into the northern two thirds of South America. Husson (1962) restricted the type locality to Martinique and Dolan (1989) applied the name *M. m. molossus* to this species in the Lesser Antilles. Genoways et al. (1981) and Timm and Genoways (2003) identified significant morphological variation among Antillean populations of *M. molossus*.

Lindsey and Ammerman (2016) studied the genetic diversification within *M. molossus* using the mitochondrial gene cytochrome-*b* from 54 individuals from throughout its geographic range. They found that all Antillean populations except those from Cuba grouped in a single clade along with individuals from several countries in South America. They recovered a low genetic divergence value of 1.2% for the individuals in this clade from across this broad geographic area. This revealed far less divergence than has been recovered from morphological studies in which nine subspecies were recognized by Simmons (2005). Although the sample from Central America consisted of only two individuals from El Salvador, these individuals fell into another clade with individuals from Brazil. This

would lend support to the hypothesis that *M. molossus* invaded the Antilles from northern South America, possibly from the area of Guyana/Suriname.

Table 1 provides the length of forearm and seven cranial measurements for 18 females and 19 males of *M. molossus* from St. Vincent. Male values were significantly larger than females for all measurements. Four of the measurements (length of forearm, greatest length of skull, condylobasal length, and mastoid breadth) differed at the $P \leq 0.001$ level, two measurements (zygomatic breadth and length of maxillary toothrow) differed at the $P \leq 0.01$ level, and two measurements (postorbital constriction and breadth across upper molars) differed at the $P \leq 0.05$ level.

These insectivorous bats were observed at nearly every site we visited on St. Vincent and were readily identified by their rapid and darting flight as they hawked their prey in twilight. This may be the most abundant species of bat on the island (Fig. 20). However, our sampling clearly underestimates their populations because we observed many more at altitudes above the reach of our mist nets. This bat was captured at 13 net sites and represented 9.4 % of total captures. These mastiff bats in modern times find day roosts under tile and corrugated steel roofs and in the attics of homes and other buildings. Before human settlement, mastiff bats would have found day roosts in tree holes and rock crevices and were probably much less common than at present.

We captured 50 of these mastiff bats at the Milikin Bay site. This area was located between a large landfill and the beach. It was dominated by a dense growth of mangrove trees that bounded a small brackish stream that cut through broad muddy banks. These bats were probably traversing this site from day roosts in the adjacent buildings out into foraging areas. Although this area did not look like typical bat habitat, we caught three other species at this site: *G. longirostris*, *A. schwartzi*, and *S. paulsoni*.

An excellent example of a natural area away from human structures and away from water where we captured *M. molossus* was on Mt. St. Andrew to the east of Pembroke where we netted three individuals of this species. The field site was along the steep, narrow

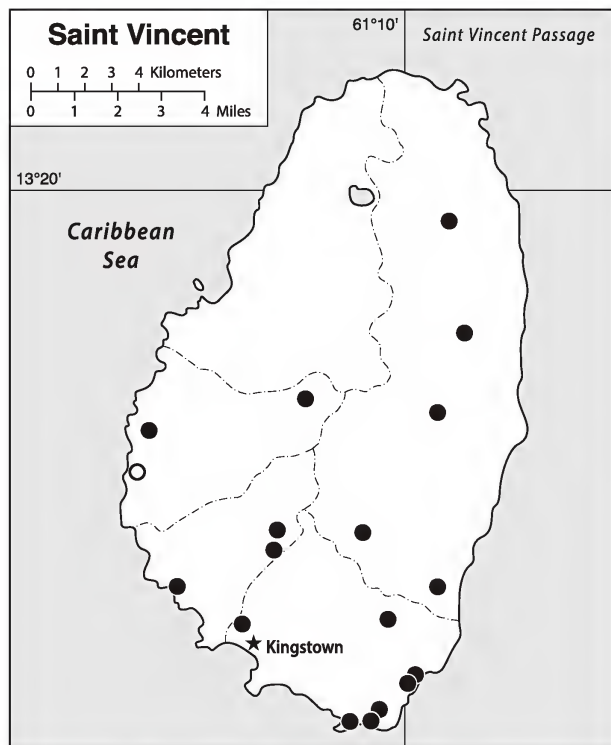


Figure 20. Map of the geographic distribution of *Molossus molossus* on the Lesser Antillean island of St. Vincent. Closed circles represent specimens examined and open circles represent literature records.

road leading to the top of Mt. St. Andrew. On one side of the road was a steep, upward-sloping open field and on the other side was a steep downward slope that was too steep to climb. Five mist nets were placed within a relatively small area with the nets set across the road, in a patch of *Piper*, under a fig tree, and a long net (18 m) was stretched between two unidentified trees. Two mastiff bats were caught in a net across the road and one was taken under the fig tree. These bats may have been foraging or simply traveling from one area of the island to another. With 36 individuals obtained, *A. schwartzi* was by far the most abundant species taken at this site, with other species represented by two individuals—*S. paulsoni*—or a single specimen—*G. longirostris*, *M. plethodon*, and *A. nicholli*.

Of the 83 female mastiff bats taken on St. Vincent during late May and early June, only one did not evince

gross reproductive activity, two were post-lactating, 59 were lactating, and 21 were pregnant, with nine of the embryos measuring a mean of 19.7 (14.0–27.5) in crown-rump length. Seven males taken during this period had their testes in a scrotal position, with two having testes that measured 5 and 6 in length and one had its testes in an inguinal position. Of the 68 females taken during late July and early August, 32 did not appear to be reproductively active, eight were post-lactating, 23 were lactating, four were pregnant, with one carrying an embryo measuring 11 in crown-rump length, and two were lactating and also carried embryos that measured 7 and 13 in crown-rump length. Nineteen males taken during this period had their testes in scrotal position of which 13 had a mean length of testes of 4.3 (2.5–6.0) and four had testes in an inguinal position, with one having testes measuring 2.0 in length. Males and females of this species were found to be at various stages of reproduction or reproductively inactive during the same periods on Jamaica (Genoways et al. 2005) and St. Martin (Genoways et al. 2007b), suggesting an aseasonal polyestrous reproductive pattern (Wilson 1979). Hayssen et al. (1993) found that females of *M. molossus* were seasonally monoestrous, but could be seasonally polyestrous in the southern parts of their geographic range, whereas males were considered seasonally spermatogenic, with scrotal males found in both winter and spring months. Our data from St. Vincent are not extensive enough to make any definitive conclusions on the reproductive cycle, but the information does not rule out aseasonal polyestry, and some type of seasonal monoestry seems to be a hard fit.

The mean body weight of 13 pregnant females captured in late May and early June was 12.0 (8.9–13.6), a lactating female weighed 11.5, whereas three mature males weighed 11.0, 11.0, and 14.2. The mean body weight of 15 lactating females netted in late July and early August was 9.9 (8.5–11.9), five non-reproductively active females weighed an average of 10.2 (9.0–12.8), two post-lactating females weighed 8.7 and 10.2, and two pregnant females weighed 9.6 and 10.0. The mean body weight of 12 males with testes in scrotal position at the end of July and beginning of August was 12.2 (10.2–13.6).

Tadarida brasiliensis antillularum (Miller, 1902)

Brazilian Free-tailed Bat

Specimens examined (12).—**St. Andrew Parish:** Waterworks, 1.25 km N, 1.6 km E Vermont, 310 m [13°12'35.6"N, 61°12'52.0"W], 1 (TTU 105478). **St. Patrick Parish:** Wallilabou Falls, 0.6 km E Wallilabou, 55 m [13°14'54.2"N, 61°15'37.7"W], 9 (TTU 105560–66, 106001–02); Wallilabou River Gorge, 0.1 km S, 1.8 km E Wallilabou, 170 m [13°14'31.7"N, 61°15'8.0"W], 2 (TTU 105581–82).

Additional records.—**St. Patrick Parish:** near mouth of Wallilabou River [≈13°14'54"N, 61°16'09"W] (Vaughan 1995; Vaughan and Hill 1996).

Based on a holotype from Roseau, Dominica, individuals of *T. brasiliensis* in the Lesser Antilles were thought to be smaller than those in the Greater Antilles and were named *Nyctinomus antillularum* by Miller (1902). He assigned specimens from Montserrat, St. Kitts, St. Lucia, and Tobago to this new taxon. In his revision of the genus *Tadarida*, Shamel (1931) treated this species under the name *Tadarida antillularum* and added material from Antigua, Guadeloupe, and Puerto Rico to this monotypic species. Schwartz (1955) reduced this species to subspecific rank within the widespread mainland species *Tadarida brasiliensis*. Although several closely related subspecies of this free-tailed bat can be found in the Antilles, *T. b. antillularum* was considered to be distributed from Puerto Rico southward as far as St. Vincent (Schwartz 1955), the southernmost population in the West Indies. At present *T. brasiliensis* is unknown from the Grenadines (Genoways et al. 2010), Grenada (Genoways et al. 1998), northeastern South America, and Trinidad. There is a single specimen known from Tobago collected in 1901 by F. A. Ober (NMNH 102073), but the species has not been taken there since that time (Goodwin and Greenhall 1961). As indicated by Timm and Genoways (2003), there were subtle morphological variations among Antillean populations that separate the subspecies *T. b. antillularum* and *T. b. constanzae* (from Hispaniola).

Owen et al. (1990) analyzed the relationships within and between mainland and Caribbean populations of *T. brasiliensis* using morphometrics and protein

electrophoresis, especially of the esterase-2 locus. They found that *T. b. cynocephala* of the southeastern United States and *T. b. mexicana* of the southwestern United States and Mexico could represent separate species based on larger cranial size of *T. b. cynocephala* and different alleles for the esterase-2 locus. Based on their results they believed that the Antillean population grouped with *T. b. cynocephala*. There is great need for a modern molecular phylogenetic analysis of the entire *Tadarida brasiliensis* complex including those in the Caribbean basin. If Owen et al. (1990) supposition about the relationships of Antillean free-tailed bats is true, it represents a unique invasion of the West Indies from the north (Rodríguez-Durán and Kunz 2001).

Length of forearm and seven cranial measurements are provided in Table 1 for five males and seven females of *T. brasiliensis*. Our analyses indicated no significant secondary sexual differences in any measurement. Females averaged larger in length of forearm, greatest length of skull, condylobasal length, mastoid breadth, and postorbital constriction, whereas males averaged greater in breadth across the upper molars, and the sexes averaged the same for zygomatic breadth and length of maxillary toothrow.

We captured only 12 *T. brasiliensis* on St. Vincent, all of which were netted over water—Waterworks, Wallilabou River Falls, and Wallilabou River Gorge (Fig. 16). The Waterworks was a water purification complex composed of three concrete settling tanks (approximately 30 m by 30 m). The upper tank that held water was populated by small shrimp. We erected four long nets (three of 12 m and one of 18 m) across the top of the upper tank. Despite the ease of bat access to the water surface and the amount of net we expended, we had poor success, taking only the single *T. brasiliensis* and six *M. molossus*. Two other nets were placed nearby along a narrow trail along a steep ridge 100 m to the northeast of the tanks. Those nets were active and captured individuals of four species—*M. buriri*, *G. longirostris*, *A. schwartzi*, and *S. paulsoni*.

Wallilabou River Falls (Fig. 21) were located adjacent to the Leeward Highway 0.6 km upstream from Wallilabou. These falls were created by large boulders of bedrock and exposed bedrock with a drop of approximately 4 m accomplished in two stages. The

swift-moving Wallilabou River was about 2.5 m wide at this point when we worked here (6 August 2005 and 6 June 2006), although there was ample evidence that much more water comes down the river at other times. The falls broke the river into three separate branches that rejoined 20 m downstream. A well-developed riparian forest formed a distinct canopy and provided a protected flyway over the river. Some of the major trees in the area included helecho gigante, waterwood, crabwood, cabbage bark, and the milktree with its extensive buttressed root. Below the falls, a huge fig tree (probably *Ficus insipida*) dominated the immediate area. At the northern base of the falls, there was a calm pool of water measuring 4 m by 3 m, which was bordered by dense vegetation on two sides. We captured nine free-tailed bats in a net placed over this pool in both 2005 ($n=2$) and 2006 ($n=7$). Other nets were placed above the falls, between the highway and the falls, and under the large fig tree below the falls. These nets captured the following species: *N. leporinus* (1), *P. fuscus* (1), *G. longirostris* (13), *A. schwartzi* (132), *S. paulsoni* (2), and *M. molossus* (20).

About a kilometer upstream from the Falls site was our Wallilabou River Gorge collection site where we took *T. brasiliensis* on the evening of 6 August 2006. The densely-vegetated ravine that contained the river above this point became progressively deeper with high rocky cliffs further upstream. A small trail followed the river upstream until it reached two boulders that were large enough to block the ravine. One net was set on the entrance trail and three in the general area of the boulders—in a clearing on the river, in a stand of *Piper*, and on rocks near the river. It was in these nets that two free-tailed bats were captured along with two *P. fuscus*, two *G. longirostris*, 27 *A. schwartzi*, and eight *S. paulsoni*.



Figure 21. Photograph of part of Wallilabou Falls, St. Patrick Parish, St. Vincent. Nine *Tadarida brasiliensis* were taken in a net placed over this pool formed by the waterfall.

The four adult females taken on 6 June 2006 were pregnant carrying embryos measuring 12, 14, 16, and 17, whereas one captured on 6 August 2005 was lactating. Two adult males obtained on 28 May and 6 June 2006 had testes in an inguinal position, both with testes measuring 4 in length, whereas four males collected on 6 June 2006 had their testes in scrotal position, with two having testes measuring 4 in length. Mainland populations of this species are monestrus producing a single offspring in May–June and fledging them generally by early August (LaVal 1973; Wilkins 1989). Insular populations appear to follow this pattern as well (Genoways et al. 2005).

Four pregnant females taken on 6 June weighed 8.2, 9.0, 9.5, and 9.6, whereas a lactating female captured on 6 August weighed 7.6. Six males taken in late May and early June had a mean weight of 8.1 (7.6–8.5).

DISCUSSION

Faunal composition.—The chiropteran fauna of St. Vincent consists of 12 species from four families: Noctilionidae (1), Mormoopidae (1), Phyllostomidae (8) and Molossidae (2). This island bat fauna represents four trophic guilds as follows: *N. leporinus* (piscivore/insectivore); *G. longirostris* and *M. plethodon* (nec-

tarivore/pollenivore); *A. lituratus*, *A. schwartzi*, *B. cavernarum*, *A. nicholli*, *S. paulsoni* (frugivore); and *P. fuscus*, *M. buriri*, *M. molossus*, and *T. brasiliensis* (insectivore). In terms of number of species, the St. Vincent bat fauna is comparable in size to several of the other larger islands in Lesser Antilles—Martinique

(11 species; Barataud et al. 2011, Issartel and Leblanc 2004), Dominica (12 species; Genoways et al. 2001), and Guadeloupe (12 species; Baker et al. 1978).

An important aspect with respect to the evolutionary history of the island's bat fauna is that four species (*A. nicholli*, *A. schwartzi*, *M. buriri*, and *M. plethodon*) are endemic to the Lesser Antilles and *Brachyphylla cavernarum* only occurs outside of the Lesser Antilles on Puerto Rico and the Virgin Islands. Two endemic species—*A. schwartzi* and *M. buriri*—are notable because available genetic and morphometric data indicate these species evolved on St. Vincent (P. Larsen et al. 2010, 2011). Also represented in the fauna are two subspecies (*A. n. vincentensis* and *S. p. paulsoni*) that are restricted to St. Vincent (Velazco and Patterson 2013; R. Larsen et al. 2017). This level of endemism is comparable to that of the central Lesser Antillean islands of Martinique and Dominica (five Lesser Antillean endemic species), but is less than that of Guadeloupe (seven Lesser Antillean endemic species), where “most of the evolutionary activity in the Lesser Antillean bat faunas has been associated” (Baker and Genoways 1978; Baker et al. 1978).

Another important aspect concerning the Lesser Antillean endemics that occur on St. Vincent is that three genera (*Ardops*, *Brachyphylla*, and *Monophyllus*) reach their southernmost Caribbean distributions on St. Vincent. The paucity of Lesser Antillean endemics on islands to the south of St. Vincent (that is, the Grenadines and Grenada) provides support for the hypothesis that the southeastern boundary of the West Indian Faunal subregion known as Koopman's line (*sensu* Genoways et al. 1998) is concomitant with the Bequia Channel between Bequia and St. Vincent (Genoways et al. 2010). The Bequia Channel is narrow currently, being only 14-km wide and may have been somewhat narrower in the Pleistocene (Fig. 2), but it always remained open during the Pleistocene having a depth of 1,100 m. The Grenadine islands lie to the south of the channel and connect Bequia to Grenada along the Grenada Bank, and then to Tobago, Trinidad, and the mainland of South America (Fig. 1). The Grenadines lie on a north-south axis and are physiographically different from St. Vincent because they form an archipelago of low-lying xeric islands.

The geographic location of St. Vincent, combined with its diverse ecology, give the island a unique and important role in Caribbean biogeography. Although the Grenadines appear to connect St. Vincent with Grenada, the stepping stone geographical arrangement may be misleading. We (Phillips et al. 1989) previously discussed our thinking about the Grenadines acting as “filter” and their collective role in limiting colonization. In so doing, we imagined multiple ongoing colonization attempts from south to north through the Grenadine archipelago. Extinctions and failures would be expected in high prevalence based on lack of food, fresh water, or roost sites, thereby influencing which species were most likely to successfully colonize St. Vincent from northern South America (Phillips et al. 1989).

Origins of the St. Vincent bat fauna.—Determining the origins of the bats of St. Vincent requires a consideration of the regional geology and the origins of the entire Caribbean bat fauna (Fig. 1). The volcanic Lesser Antillean islands, including St. Vincent, emerged from the Caribbean Sea < 40 mya; the Lesser Antilles have never been connected to mainland North America or South America. Moreover, many of the islands have never been connected with each other, with the exception of those on shallow interconnected Pleistocene banks (for example, Anguilla, St. Martin, and St. Bart's on St. Martin Bank; Antigua and Barbuda on Barbuda Bank; St. Eustatius, St. Kitts, and Nevis on St. Kitts Bank; Grenadines and Grenada on Grenada Bank; Ricklefs and Bermingham 2008; Fig. 2). Knowing this, the most likely explanation for the geographic origins of Lesser Antillean bats is colonization by over water dispersal, perhaps mediated by prevailing trade winds, storm tracks, or disturbances (Hedges 1996, 2001; Genoways et al. 2005; Dávalos 2009; Pedersen et al. in press). The endemic Lesser Antillean bat fauna must have evolved from Greater Antillean or mainland ancestral stocks. Extensive molecular and morphological data support the hypothesis that several colonization routes have contributed to the extant Lesser Antillean fauna, with source populations located on mainlands: Central America, including Mexico (via the Greater Antilles); northern South America and Trinidad; and North America via Florida (Baker and Genoways 1978; P. Larsen et al. 2011; Dávalos and Turvey 2012; R. Larsen et al. 2012; Tavares et al. 2018).

Given the geographic location of St. Vincent in the southern Lesser Antilles, it would be expected that bat species colonized the island following a stepping stone model from either the north via Martinique and St. Lucia or the south via the Grenadines. Using a combination of published phylogenetic and morphometric data, we can hypothesize as to the general geographic origin of each of the 12 species that occur on St. Vincent: *B. cavernarum*, *M. plethodon*, *A. nicholli*, and *T. brasiliensis* likely colonized St. Vincent from the north (Baker and Genoways 1978; Swanepoel and Genoways 1978; Owen et al. 1990; Carstens et al. 2004; R. Larsen et al. 2017), whereas *N. leporinus*, *G. longirostris*, *A. lituratus*, *P. fuscus*, *S. paulsoni*, and *M. molossus* likely colonized from the south (Hoffmann and Baker 2001; R. Larsen et al. 2013; Khan et al. 2014; Lindsey and Ammerman 2016). Owen et al. (1990) analyzed the relationships between mainland and Caribbean populations of *T. brasiliensis* using a combination of phenotypes—morphometrics and protein electrophoresis of the esterase-2 locus. They found that *T. b. cynocephala* of the southeastern United States grouped with Antillean populations, indicating a potential invasion of the islands from North America north of Mexico, but via Florida rather than from the Central American mainland.

The foregoing overview leaves the two endemic species on St. Vincent, *Artibeus schwartzi* and *Micronycteris buriri*. The origin of *A. schwartzi* is complex and likely involves hybridization among several species of *Artibeus* originating from both the northern Lesser Antilles and northern South America (see *A. schwartzi* species account). The ancestor of *M. buriri* most likely colonized St. Vincent from the south during the late Pleistocene when vast portions of the Grenada Bank were exposed (P. Larsen et al. 2011).

With respect to the entire St. Vincent bat assemblage, the individual colonization histories are incredibly fascinating in that each species established populations on the island at different points in time, with some species being old colonizers (for example, *P. fuscus*, *S. paulsoni*) and some young (for example, *A. nicholli*, *M. buriri*). Moreover, it is highly likely that multiple waves of colonization events for individual taxa have occurred (for example, *Artibeus*). It has been proposed that climate, sea level changes, and loss of

island area since the last glacial maximum (LGM) have reduced habitat resulting in extirpations and extinctions (P. Larsen et al. 2011; Dávalos and Russell 2012; R. Larsen et al. 2017). A comparison of land areas before and after the LGM (Fig. 2), indicate a minor shrinkage of land area on St. Vincent following glacial melt and sea level rise. Based on radiocarbon dates of bat fossils and time-scale ecological niche models, it has been hypothesized that reduced island size is not a cause of bat extinctions and extirpations, but prehistoric and historic human impacts (for example, predation, habitat alteration, fire, invasive species) more likely caused bat population declines (Soto-Centeno and Steadman 2015; Valente et al. 2017). There is no fossil history available for the bats of St. Vincent and therefore genetic analyses of the extant fauna are required to test biogeographic hypotheses regarding origins. Modern population genomic approaches, such as coalescent analyses using genome-wide sequence data, can provide resolution into these complicated histories and we recommend future studies that leverage the power of modern genomic tools to gain a better understanding of the evolutionary histories of Lesser Antillean bats. Such tools also could be used to test hypotheses about the filtering potential of the Grenadines and this in turn could enable us to describe the effect of filtering on population genetics.

Disturbances.—The Caribbean is influenced by ocean-atmospheric interactions that result in high cyclonic (hurricane) activity (Landsea et al. 1999) that track in the direction of surface current flow (Hedges 2006). Paleoclimatologists indicate the Intertropical Convergence Zone (ITCZ: where northeast and southeast trade winds meet) has oscillated in latitude at least twice during the last 10,500 years (Hodell et al. 1991) and is responsible for shifting wind and precipitation patterns. Hurricanes provide physical disturbance to land and sea, resulting in changes in biotic distributions via flotsam and jetsam (Walker 1991; Hedges 2006). Currently, most storms develop over the Atlantic Ocean and enter the Caribbean from the southeast and move towards the northwest; this pattern provides a strong directionality for over-water dispersal. Despite this southeast to northwest directionality, all Caribbean hurricanes ultimately turn and dissipate over the central or northern Atlantic Ocean. The counterclockwise airflow of the hurricane vortex creates strong outer rainbands

with winds that can reach out several hundred kilometers. These winds as they curl around the eye of the storm are moving north to south and then returning to the north, which may be a factor for dispersal southward at least from one island to the next as well as moving species northward (Hedges 2006; UNIDATA 2017). Island animal populations are generally small with reduced genetic diversity (Frankham 1996, 1998), and hurricanes are reported to further reduce populations of both West Indian birds and bats (Askins and Ewert 1991; Waide 1991; Pedersen et al. 1996; Barlow et al. 2000; Fleming and Murray 2009). Populations of phyllostomid bats on Puerto Rico were reduced to 25% or less of pre-hurricane numbers after hurricanes Hugo and Georges (Gannon and Willig, 1994; Jones et al. 2001; Rodriguez-Duran and Vazquez 2001) with a reduction in fruit availability for consumption (Rodriguez-Duran and Vazquez 2001).

Reports of long-distance dispersal of birds by hurricanes (Marble 1939; Tuck 1968) were hypothesized to be carried in the eye of the hurricane where winds are relatively calm, rather than in the strong forced winds in the outer rainbands, and the updrafts within the eye aid in keeping the birds airborne. Recently birds have been observed on radar in the eye of hurricanes (Philippsborn 1999; Antonio 2016); therefore, we conclude that it is probable that medium to large bats can be transported in similar fashion.

Volcanic activity on St. Vincent is another important natural disturbance. Eruptions on St. Vincent occurred in 1902 and 1979. This volcanic activity, however, is not much different than that described for Guadeloupe, Dominica, and Martinique, and more recently on Montserrat (since 1995 and ongoing) where aerial insectivores including molossid and natalid bats are part of the current fauna. Volcanoes alter the topography, habitat, and refugia on all these islands, but as we have found on Montserrat after an eruption and associated pyroclastic flows destroyed habitats on as much as half of the island, populations of the 10 species of bats known from the island were still present (Pedersen et al. 1996; R. Larsen et al. 2007). There are no demonstrable differences among these volcanic islands that would explain the current distributions of aerial insectivores.

The species of bats that inhabit the Lesser Antilles and certainly those of St. Vincent are adapted to disturbance ecosystems. To review, the major disturbances that occur throughout these islands on a relatively regular basis include hurricanes and other tropical storms, trade winds, floods, volcanic eruptions and associated pyroclastic flows, earthquakes, landslides, droughts, and in the last 2500 years, human impacts. These forces do help increase the biological diversity of these islands by opening areas in climax plant communities that allow pioneer and succession communities to develop. Ecological disturbances also can have an important genetic effect by introducing new genotypes into an island population (Fleming and Murray 2009). With trees stripped of foliage and fruits and insects blown away, it would be expected that some species of bats will have higher survival/extinction rates than others. Although virtually no empirical data are available, it seems likely that survival probability is most influenced by metabolism. There are some hints in older work on comparative physiology (McNab 1969) that Caribbean species of phyllostomids might have unique features and capabilities.

Island species richness.—The number of bat species, or species richness, on islands results from an unknown number of factors thought to include disturbances, immigration, emigration, extinction, distance to source pools (neighboring islands and continental land masses), habitat diversity, and island area (MacArthur and Wilson 1963, 1967; Pedersen et al. 2006, 2009, in press; Willig et al. 2009). Diversity of habitats can be related to elevation, but species diversity relative to elevation is variable depending on taxon. The most consistent and widely used indication of island species richness is island area (MacArthur and Wilson 1963, 1967; Sánchez-Cordero 2001; McCain 2005; Pedersen et al. 2006, in press; Willig et al. 2009). In recent analyses of the Lesser Antillean bat faunas, the 12 species of bats on St. Vincent hold a place above the species-area regression line relative to other Lesser Antillean bat faunas (Genoways et al. 2005; Pedersen et al. 2006, 2009; see Fig. 17 in Pedersen et al. in press). In fact, St. Vincent is not only located above the regression line but above the upper 95% percentile line, thus indicating that it is significantly species-rich in comparison to Martinique and St. Lucia and other Lesser Antillean islands, but it is matched by Grenada from south of Koopman's Line.

This may be due to the unique position of St. Vincent in the southern Lesser Antilles, serving as a transition zone between the Antillean and the Neotropical South American faunas. The diversity of extant bat species observed on St. Vincent may be related to its relative closeness to South America.

Elevation also is impacting the diversity of the bat fauna on St. Vincent as shown by the species-elevation regression, which placed the island above the upper 95% percentile line (see Fig. 16a in Pedersen et al. in press). Not only is elevation important but also elevational gradients, which create steep mountain ridges and rugged terrain that prevent development by humans. It is most likely that a combination of some or all of these factors is important and has influenced species diversity/richness. However, St. Vincent's geophysical position also may be unfavorable for species moving southward due to distance and the width of the passage that separates St. Vincent from St. Lucia, just as a water-gap is a barrier to northward dispersing species.

Although the bat fauna of St. Vincent has high species richness, there are potentially other species that could be present on the island. Three species of *Myotis* occur in the Lesser Antilles—*M. dominicensis* (Dominica and Guadeloupe), *M. martiniquensis* (Martinique), and *M. nyctor* (Barbados and Grenada)—with presumed ancestors entering the islands from South America (R. Larsen et al. 2012); however, during our work on St. Vincent, no member of the genus was captured. R. Larsen et al. (2012) believed that the species of *Myotis* represented at least two invasions of the Lesser Antilles. If these species, or their ancestors, invaded the islands in a stepwise manner, then both invasions could have passed through or over St. Vincent as well as St. Lucia where surveying efforts as of yet have not been able to confirm their presence (Pedersen et al. in press). If these bats did travel via St. Vincent, it would appear that they did not overcome the barriers of establishment and reproduction on the island. The presence of *M. nyctor* on Grenada and Barbados suggests an alternate route northward with species passing through the filter of the Grenadines to Barbados rather than St. Vincent. Both St. Vincent and St. Lucia could be skipped on this route with species passing north from Barbados to Martinique (Fig. 1).

Another southern species that appears to have bypassed, or gone locally extinct, on St. Vincent is *Pteronotus davyi*, which is known to occur on Trinidad, Grenada, St. Lucia, Martinique, Dominica, and Marie Galante; however, it is absent from St. Vincent, the only island where *P. fuscus* occurs. Pedersen et al. (in press) suggested that this could be an example of the priority effect or progression rule (Steinbauer 2016; Waters 2011), where overlap in prey items or competition for limited roost sites could have reduced the likelihood of one of the species inhabiting the island.

There are four additional species—*Peropteryx macrotis*, *Micronycteris megalotis*, *Anoura geoffroyi*, and *Dermanura* sp.—that have made the dispersal to Grenada from South America, but have not currently made the move further northward (Genoways et al. 1998). *Peropteryx macrotis* is the only member of the pan-tropical chiropteran family Emballonuridae (21 Neotropical species) to occur on any of the islands in the Lesser or Greater Antilles. Although *Micronycteris megalotis* (*sensu stricto*) is not present on St. Vincent, our hypothesis is that the common ancestor of *M. megalotis* and *M. buriri* colonized St. Vincent and subsequently evolved species-level characteristics therefore warranting the binomial *M. buriri* (P. Larsen et al. 2011). *Anoura geoffroyi* is a pollenivorous/nectivorous species and it shares Grenada with another species with very similar dietary requirement, *Glossophaga longirostris*. The latter species is common on the Grenadine islands and St. Vincent, thus given sympatry on Grenada, the absence of *A. geoffroyi* on St. Vincent may simply be a function of colonization time (that is, colonized Grenada from the south more recently than *G. longirostris* and has yet to establish a viable population on St. Vincent) or its absence could be another case of the progression rule. *Dermanura* sp. is a fruit-eating species, which is the only representative of this widespread Neotropical genus (12 species) in the Lesser or Greater Antilles. It is unknown whether or not colonization time or resource competition from the larger fruit-eating species of the genus *Artibeus* has resulted in this species being absent on St. Vincent.

To the north, eight of the nine species of bats on St. Lucia are represented on St. Vincent, with the exception being *P. davyi* (Pedersen et al. in press).

Martinique is the next island to the north, with three species of the 11 known from the island not represented on St. Vincent—*P. davyi*, *M. martiniquensis*, and *Natalus stramineus* (Issartel and Leblanc 2004; Barataud et al. 2011). All three of these species have an insectivorous diet. *Natalus stramineus* is a Lesser Antillean endemic occurring as far north as Anguilla (Fig. 1); this small-bodied species may appear delicate in build but is clearly adapted to the disturbance ecology of these islands. It is unknown whether the absence of *N. stramineus* on St. Vincent is a function of colonization time, local extinction, failure to cross the St. Lucia Channel, or other reasons.

Adaptability of bats.—The traditional ways of thinking about dispersal and colonization of the Antillean islands by bats focused on the idea of bats following wind currents aloft or becoming caught in updrafts of storms and assisted in making a flight from mainland to island or one island to another (Carstensen et al. 2012; see Pedersen et al. [in press] for extended discussion of this topic). Following such a flight, the arriving bat(s) might join the local fauna, so long as mating and production of young was successful. Distributional patterns that emerged from collecting bat specimens, especially in the Caribbean, have been attributed to a variety of factors, excluding the possibility of being random (Pedersen et al. in press). Clearly, it is time to take a fresh look at the process of island dispersal by Caribbean bats and begin to develop new testable hypotheses that take advantage of modern genomic datasets and modern evolutionary biology. In part, we think that the discovery of a novel, “hybrid” species of *Artibeus* on St. Vincent illustrates the importance of reconsidering our ideas on island speciation. More important, the discovery of *Artibeus schwartzi* on St. Vincent is consistent with the recent report of rapid hybrid speciation in Galápagos finches (Lamichhaney et al. 2017). In the case of the finches, it was found that reproductive isolation was established in only three generations. Such a finding is surely important and supports pursuit of new ways to investigate the biogeographic history of bats in the Caribbean.

When thinking of the establishment of incipient populations on isolated insular systems there are at least three topics to consider: 1) models derived from studies of invasive species can be applied to island dispersal and colonization questions; 2) dietary, metabolic, and

other physiological requirements of potential colonizers are critical factors to the successful colonization of a novel habitat; and 3) phenotypic plasticity and rapid local adaptation is key to successful island colonization, especially across ecologically heterogeneous insular systems. All three of these topics are interrelated, but yet different enough that appropriate hypotheses would be testable without overlap and would provide new ways of visualizing dispersal from mainland to islands, *vice versa*, and among islands.

In principal, island colonization by bats is roughly analogous to the biological factors associated with invasive species (Lucek et al. 2012). In the case of invasive species, attention has been paid to establishment of colonies that might or might not persist over time. Fairly recently, a testable hypothesis called “propagule pressure” has been developed around colonization following dispersal (Williamson and Fitter 1996; Colautti et al. 2006; Simberloff 2009; Blackburn et al. 2011). Although this hypothesis was developed around human-controlled releases of animals into new locations, it nonetheless can be adapted to island colonization under natural conditions. A good example of rapid evolution following dispersal and successful colonization of islands was uncovered by Velo-Antón et al. (2012), who studied the evolution of an alternative reproductive pathway (viviparity) in insular fire salamanders. Overall, this project documented how rapid evolution can occur in island populations derived from a propagule.

Thinking in terms of propagules and propagule pressure(s) reminds us that each propagule faces its own set of pressures, which in bats probably includes habitat (shelter and microclimate), resource availability on a year-around basis, and numbers of individuals. By tradition, food availability on islands has been taken for granted, whereas the unusual physiology of bats has rarely, if ever, been factored into discussions of island populations. Food—collectively “diet”—is treated very simply. Insectivorous bats eat insects and frugivorous species eat fruit and so forth. Actually, however, the unusual physiology of most species of bats and their diverse diets combine under the category of metabolism and operate across complex levels of gene expression, RNA regulatory elements, proteins and protein-protein interactions. For example, when we think of insectivorous bats colonizing Antillean

islands, it also is necessary to think in terms of all the molecular processes that provide access to the lipids that are required for metabolic fuel.

To consider what might happen to bats that occur in the Caribbean, we use the example of the evolution of metabolic systems because dietary diversity is a hallmark of bat evolution. Unlike many mammals, most (or all) Microchiroptera (microbats) are heterothermic, which means that they allow their basal temperature to fluctuate in the course of a 24-hr cycle. More important, microbats have unique, far more complicated metabolism than do most other mammals. Daily torpor, for example, requires that cells can tolerate anoxia. Moreover, the energetic demands of flight are such that oxidation of fatty acids is far more important as a source of metabolic energy for flight muscles than is glycolysis (Yacoe et al. 1982; Powers et al. 1991). In fact, in bats it appears to be the case that lipids are by far more important than carbohydrates, which partly can be explained by the energy density of stored fat versus glycogen (Powers et al. 1991). It also has been shown that bats have numerous genetic-based modifications that enable them to quickly access ingested lipids to provide energy needed for flight (Phillips et al. 2014).

The early research on skeletal muscle metabolism in bats was conducted in the 1980s. Since then research has been limited, but, genomic datasets now open the door to new ways to look at basic questions about metabolic processes in bats. In comparison to evidence of oxidative processes, very few fast glycolytic (FG) fibers were observed in any of the muscles studied. Such a finding emphasizes the importance of oxidative metabolism in the flight muscles (Hermanson and Foehring 1988). Our hypothesis is that metabolic pathways are the key to understanding dispersal and propagule success through adaptation in bats. But for this to be the case, it would require that associated

pathways are flexible and able to rapidly adapt to novel environments.

Final observations.—Considering all of the available data, the chiropteran fauna of St. Vincent is unique in several areas of zoogeography and taxonomy. Two species have evolved on the island—*Micronycteris buriri* and *Artibeus schwartzi*. The latter is hypothesized to have originated from reticulate evolution, a poorly understood phenomenon in mammals involving hybridization among two or more taxa (see *A. schwartzi* species account; P. Larsen et al. 2010; Amaral et al. 2014). This is emblematic of the crossroads nature of the bat populations on St. Vincent. There are also two endemic subspecies of bats on the island—*A. n. vinctensis* and *S. p. paulsoni*. This degree of endemism at both the species and subspecies levels is an indication of the isolation of the island as well as the adaptability of the bats species themselves.

St. Vincent is the northern-most outpost for three species that have moved into the Lesser Antilles from northern South America—*P. fuscus*, *G. longirostris*, and *A. lituratus*. It is the southern-most outpost for four species of bats that would have reached the island by moving southward—*M. plethodon*, *B. cavernarum*, *A. nichollsi*, and *T. brasiliensis*. The first three of these species are Antillean endemics so that St. Vincent represents the southern limit of the Lesser Antillean bat fauna.

The characteristics of the bat fauna of St. Vincent—a crossroads for species, an outpost for both northern and southern species, the boundary for a multi-island bat fauna as marked by Koopman's Line, and a site of endemism—are unique in the West Indies. However, based on our studies, we place the bat fauna of St. Vincent as the southern-most island in the Lesser Antillean Faunal Core (Genoways et al. 2001).

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LITERATURE CITED

- Allen, G. M. 1908. Notes on Chiroptera. *Bulletin of the Museum of Comparative Zoology, Harvard College* 52:25–62.
- Allen, G. M. 1911. Mammals of the West Indies. *Bulletin of the Museum of Comparative Zoology, Harvard College* 54:175–263.
- Allen, J. A. 1911. Mammals from Venezuela collected by Mr. M. A. Carriker, 1909–1911. *Bulletin of the American Museum of Natural History* 30:239–273.
- Alonso-Mejía, A., and R. A. Medellín. 1991. *Micronycteris megalotis*. *Mammalian Species* 376:1–6.
- Amaral, A. R., G. Lovewell, M. M. Coelho, G. Amato, and H. C. Rosenbaum. 2014. Hybrid speciation in a marine mammal: the Clymene dolphin (*Stenella clymene*). *PLoS ONE* 9(1):e83645.doi:10.1371/journal.pone.0083645.
- Antonio, M. 2016. Radar spots flock of birds inside the eye of Hurricane Matthew—but why? *Nature World News*, accessed at <<https://www.natureworldnews.com/articles/29852/20161008/radar-spots-flock-birds-inside-eye-hurricane-matthew-why.htm>> on 10 May 2018.
- Andersen, K. 1908. A monograph of chiropteran genera *Uroderma*, *Enchisthenes*, and *Artibeus*. *Proceedings of the Zoological Society of London* 1908:204–319.
- Askins, R., and D. Ewert. 1991. Impact of Hurricane Hugo on bird populations on St. John, U.S. Virgin Islands. *Biotropica* 23:481–487.
- Baker, R. J., O. R. P. Bininda-Emonds, H. Mantilla-Meluk, C. A. Porter, and R. A. Van Den Bussche. 2012. Molecular timescale of diversification of feeding strategy and morphology in New World leaf-nosed bats (Phyllostomidae): a phylogenetic perspective. Pp. 385–409 in *Evolutionary history of bats: fossils, molecules and morphology* (G. F. Gunnell and N. B. Simmons, eds.). Cambridge University Press, Cambridge Studies in Molecules and Morphology—New Evolutionary Paradigms, New York.

- Baker, R. J., and H. H. Genoways. 1978. Zoogeography of Antillean bats. Pp. 53–97 in *Zoogeography in the Caribbean: The 1975 Leidy Medal Symposium* (F. B. Gill, ed.). Special Publication of the Academy of Natural Sciences of Philadelphia 13:iii + 1–128.
- Baker, R. J., H. H. Genoways, and J. C. Patton. 1978. Bats of Guadeloupe. *Occasional Papers, Museum of Texas Tech University* 50:1–16.
- Baker, R. J., S. R. Hoofer, C. A. Porter, and R. A. Van Den Bussche. 2003. Diversification among New World leaf nosed bats: an evolutionary hypothesis and classification inferred from digenomic congruence of DNA sequence. *Occasional Papers, Museum of Texas Tech University* 230:1–32.
- Baker, R. J., S. Solari, A. Cirranello, and N. B. Simmons. 2016. Higher level classification of phyllostomid bats with a summary of DNA synapomorphies. *Acta Chiropterologica* 18:1–38.
- Barker, G. H. 1981. St. Vincent, an agricultural profile. CARDI Research Project #538-0015. Caribbean Agricultural Research and Development Institute, St. Augustine, Trinidad.
- Barlow, K. E., N. Vaughan, K. E. Jones, A. Rodriguez-Duran, and M. R. Gannon. 2000. Are bats which pollinate and disperse forest plants particularly sensitive to disturbance? A case study of the effects of Hurricane Georges on bats in Puerto Rico. *Bulletin of the British Ecological Society* 31:36–39.
- Barataud, M., S. Giosa, G. Issartel, and J. Jemin. 2011. Bioévaluation des forêts de Martinique par l'étude de l'activité des guildes de chiroptères. Rapport, Direction Régionale de l'Environnement, Martinique, 32 pp.
- Beard, J. 1945. The progress of plant succession on Soufriere of St. Vincent. *Journal of Ecology* 33:1–9.
- Beard, J. 1949. The natural vegetation of the Windward and Leeward Islands. Clarendon Press, Oxford.
- Bermingham, E., G. Seutin, and R. Ricklefs. 1996. Regional approaches to conservation biology: RFLPs, DNA sequence, and Caribbean birds. Pp. 104–124 in *Molecular genetic approaches in conservation* (T. B. Smith and R. K. Wayne, eds.). Oxford University Press, New York.
- Birdsey, R., P. L. Weaver, and C. F. Nicholls. 1986. The forest resources of St. Vincent, West Indies. Research Paper SO-229, United States Department of Agriculture, Forest Service, Southern Forest Experiment Station, New Orleans, LA.
- Blackburn, T. M., P. Pyšek, S. Bacher, J. T. Carlton, R. P. Duncan, V. Jarošík, J. R. U. Wilson, and D. M. Richardson. 2011. A proposed unified framework for biological invasions. *Trends in Ecology and Evolution* 26:333–339.
- Bond, R. M., and G. A. Seaman. 1958. Notes on a colony of *Brachyphylla cavernarum*. *Journal of Mammalogy* 39:150–151.
- Breuil, M. 1997. Les collections herpétologiques et chiroptérologiques du Musée du Père Pinchon. Conseil régional de la Martinique, Laboratoire des Reptiles et Amphibiens, Muséum national d'histoire naturelle, France: Fort de France and Paris.
- Breuil, M., and D. Masson. 1991. Quelques remarques sur la biogéographie des chauves-souris des Petites Antilles. *Compte Rendu de la Société de Biogéographie* 67:25–39.
- Brooke, A. P. 1994. Diet of the fishing bat, *Noctilio leporinus* (Chiroptera: Noctilionidae). *Journal of Mammalogy* 75:212–218.
- Caribbean Conservation Association. 1991. St. Vincent and the Grenadines: Country Environmental Profile. Caribbean Conservation Association, St. Michael, Barbados.
- Caribbean Hurricane Network. 2014. St. Vincent. Accessed at <<http://stormcarib.com/>> on 27 October.
- Carstens, B. C., J. Sullivan, L. M. Dávalos, P. A. Larsen, and S. C. Pedersen. 2004. Exploring population genetic structure in three species of Lesser Antillean bats. *Molecular Ecology* 13:2557–2566.
- Carstensen, D. W., B. Dalsgaard, J.-C. Svenning, C. Rahbek, J. Fjeldså, W. J. Sutherland, and J. M. Olesen. 2012. Biogeographical modules and island roles: a comparison of Wallacea and the West Indies. *Journal of Biogeography* 39:739–749.
- Cirranello, A., N. B. Simmons, S. Solari, and R. J. Baker. 2016. Morphological diagnoses of higher-level phyllostomid taxa (Chiroptera: Phyllostomidae). *Acta Chiropterologica* 18:39–71.
- Clare, E. L., A. M. Adam, A. Z. Maya-Simões, J. L. Eger, P. D. N. Hebert, and M. B. Fenton. 2013. Diversification and reproductive isolation: cryptic species in the only New World high-duty cycle bat, *Pteronotus parnellii*. *BMC Evolutionary Biology* 2013 13:26.
- Clark, P. U., A. S. Dyke, J. D. Shakun, A. E. Carlson, J. Clark, B. Wohlfarth, J. X. Mitrovica, S. W. Hostetler, and A. M. McCabe. 2009. The last glacial maximum. *Science* 235:710–714.
- Colautti, R. I., I. A. Grigorovich, and H. J. MacIsaac. 2006. Propagule pressure: a null model for biological invasions. *Biological Invasions* 8:1023–1037.
- Coyne, J. A., and H. A. Orr. 2004. Speciation. Sinauer Associates, Sunderland, Massachusetts.
- Dávalos, L. M. 2004. Phylogeny and biogeography of Caribbean mammals. *Biological Journal of the Linnean Society* 81:373–394.
- Dávalos, L. M. 2005. Molecular phylogeny of funnel-eared bats (Chiroptera: Natalidae), with notes on biogeography and conservation. *Molecular Phylogenetics and Evolution* 37:91–103.

- Dávalos, L. M. 2006. The geography of diversification in the mormoopids (Chiroptera: Mormoopidae). *Biological Journal of the Linnean Society* 88:101–118.
- Dávalos, L. M. 2009. Earth history and the evolution of Caribbean bats. Pp. 96–115 in *Island bats: evolution, ecology, and conservation* (T. H. Fleming and P. A. Racey, eds.). University of Chicago Press, Chicago, Illinois.
- Dávalos, L. M., and A. L. Russell. 2012. Deglaciation explains bat extinctions in the Caribbean. *Ecology and Evolution* 12:3045–3051.
- Dávalos, L. M., and S. T. Turvey. 2012. West Indian mammals: the old, the new, and the recently extinct. Pp. 157–202 in *Bones, clones, and biomes: the history and geography of Recent neotropical mammals* (B. D. Patterson and L. P. Costa, eds.). University of Chicago Press, Chicago, Illinois.
- Davies, N., and E. Bermingham. 2002. The historical biogeography of two Caribbean butterflies (Lepidoptera: Heliconiidae) as inferred from genetic variation at multiple loci. *Evolution* 56:573–589.
- Davies, N., and D. S. Smith. 1998. Munroe revisited: a survey of West Indian butterfly faunas and their species-area relationship. *Global Ecology and Biogeography Letter* 7:285–294.
- Davis, W. B. 1973. Geographic variation in the fishing bat, *Noctilio leporinus*. *Journal of Mammalogy* 54:862–874.
- de la Torre, L. 1966. New bats of the genus *Sturnira* (Phyllostomidae) from the Amazonian lowlands of Peru and the Windward Islands, West Indies. *Proceedings of the Biological Society of Washington* 79:267–272.
- de la Torre, L., and A. Schwartz. 1966. New species of *Sturnira* (Chiroptera: Phyllostomidae) from the islands of Guadeloupe and Saint Vincent, Lesser Antilles. *Proceedings of the Biological Society of Washington* 79:297–304.
- Ditchfield, A. D. 2000. The comparative phylogeography of Neotropical mammals: patterns of intraspecific mitochondrial DNA variation among bats contrasted to nonvolant mammals. *Molecular Ecology* 9:1307–1318.
- Dobson, G. E. 1878. *Catalogue of the Chiroptera in the collection of the British Museum*. Trustees of the British Museum, London.
- Dolan, P. G. 1989. Systematics of Middle American mastiff bats of the genus *Molossus*. *Special Publications, Museum of Texas Tech University* 29:1–71.
- Findley, J. S., and D. E. Wilson. 1983. Are bats rare in tropical Africa? *Biotropica* 15:299–303.
- Fleming, T. H., and K. L. Murray. 2009. Population and genetic consequences of hurricanes for three species of West Indian phyllostomid bats. *Biotropica* 41:250–256.
- Frankham, R. 1996. Relationship of genetic variation to population size in wildlife. *Conservation Biology* 10:1500–1508.
- Frankham, R. 1998. Inbreeding and extinction: island populations. *Conservation Biology* 12:665–675.
- Funk, D. J., and K. E. Omland. 2003. Species-level paraphyly and polyphyly: frequency, causes, and consequences, with insights from animal mitochondrial DNA. *Annual Review of Ecology, Evolution, and Systematics* 34:397–423.
- Gannon, M. R., and M. R. Willig. 1994. The effects of Hurricane Hugo on bats of the Luquillo experimental forest in Puerto Rico. *Biotropica* 26:320–331.
- Genoways, H. H. 1998. Two new species of bats of the genus *Sturnira* from the Lesser Antilles, West Indies. *Occasional Papers, Museum of Texas Tech University* 176:1–7.
- Genoways, H. H., R. J. Baker, J. W. Bickham, and C. J. Phillips. 2005. *Bats of Jamaica*. *Special Publications, Museum of Texas Tech University* 48:1–154.
- Genoways, H. H., R. C. Dowler, and C. H. Carter. 1981. Intra-island and interisland variation in Antillean populations of *Molossus molossus* (Mammalia: Molossidae). *Annals of Carnegie Museum* 50:475–492.
- Genoways, H. H., and J. K. Jones, Jr. 1975. Additional records of the stenodermine bat, *Sturnira thomasi*, from the Lesser Antillean island of Guadeloupe. *Journal of Mammalogy* 56:924–925.
- Genoways, H. H., G. G. Kwiecinski, P. A. Larsen, S. C. Pedersen, R. J. Larsen, J. D. Hoffman, M. de Silva, C. J. Phillips, and R. J. Baker. 2010. Bats of the Grenadine Islands, West Indies, and placement of Koopman's Line. *Chiroptera Neotropical* 16:501–521.
- Genoways, H. H., R. J. Larsen, S. C. Pedersen, G. G. Kwiecinski, and P. A. Larsen. 2011. Bats of Barbados. *Chiroptera Neotropical* 17:1029–1054.
- Genoways, H. H., P. A. Larsen, S. C. Pedersen, and J. J. Huebschman. 2007a. Bats of Saba, Netherlands Antilles. *Acta Chiropterologica* 9:91–114.
- Genoways, H. H., S. C. Pedersen, P. A. Larsen, G. G. Kwiecinski, and J. J. Huebschman. 2007b. Bats of Saint Martin, French West Indies/Sint Maarten, Netherlands Antilles. *Mastozoologia Neotropical* 14:169–188.
- Genoways, H. H., S. C. Pedersen, C. J. Phillips, and L. K. Gordon. 2007c. Bats of Anguilla, northern Lesser Antilles. *Occasional Papers, Museum of Texas Tech University* 270:1–12.
- Genoways, H. H., C. J. Phillips, and R. J. Baker. 1998. Bats of the Antillean island of Grenada: a new zoogeographic perspective. *Occasional Papers, Museum of Texas Tech University* 177:1–32.

- Genoways, H. H., R. M. Timm, R. J. Baker, C. J. Phillips, and D. A. Schlitter. 2001. Bats of the West Indian island of Dominica: natural history, areography, and trophic structure. Special Publication, Museum of Texas Tech University 43:1–44.
- Goodwin, G. G., and A. M. Greenhall. 1961. A review of the bats of Trinidad and Tobago. Bulletin of the American Museum of Natural History 122:187–302.
- Graham, A. 2003. Geohistory models and Cenozoic paleoenvironments of the Caribbean region. Systematic Botany 28:378–386.
- Grant, P. R., and B. R. Grant. 2014. Synergism of natural selection and introgression in the origin of a new species. American Naturalist 183:671–681.
- Grant, P. R., and B. R. Grant. 2015. Introgressive hybridization and natural selection in Darwin's finches. Biological Journal of the Linnean Society <http://dx.doi.org/10.1111/bij.12702>.
- Gray, J. E. [1833] 1834. Characters of a new genus of bats (*Brachyphylla*), obtained by the Society from the collections of the late Rev. Lansdown Guilding. Proceedings of the Zoological Society of London Part 1:122–123.
- Gutiérrez, E. E., and J. Molinari. 2008. Morphometrics and taxonomy of bats of the genus *Pteronotus* (subgenus *Phyllodia*) in Venezuela. Journal of Mammalogy 89:292–305.
- Hall, E. R. 1946. Mammals of Nevada. University of California Press, Berkeley.
- Handley, C. O., Jr., and W. D. Webster. 1987. The supposed occurrence of *Glossophaga longirostris* Miller on Dominica and problems with the type series of *Glossophaga rostrata* Miller. Occasional Papers, Museum of Texas Tech University 108:1–10.
- Hayssen, V., A. van Tienhoven, and A. van Tienhoven. 1993. Asdell's patterns of mammalian reproduction: a compendium of species-specific data. Cornell University Press, Ithaca, New York, and London.
- Hedges, S. B. 1996. Historical biogeography of West Indian vertebrates. Annual Review of Ecology and Systematics 27:163–196.
- Hedges, S. B. 2001. Biogeography of the West Indies: an overview. Pp. 15–33 in Biogeography of the West Indies: patterns and perspectives (C. A. Woods and F. E. Sergile, eds.). CRC Press, Boca Raton, Florida.
- Hedges, S. B. 2006. Paleogeography of Antilles and origin of West Indian terrestrial vertebrates. Annals of the Missouri Botanical Garden 93:231–244.
- Helmus, M. R., and A. R. Ives. 2013. Phylogenetic diversity-area curves. Ecology 93:S31–S43.
- Herd, R. M. 1983. *Pteronotus parnellii*. Mammalian Species 209:1–5.
- Hermanson, J. W., and R. C. Foehring. 1988. Histochemistry of flight muscles in the Jamaican fruit bat, *Artibeus jamaicensis*: implications for motor control. Journal of Morphology 196:353–362.
- Hershkovitz, P. 1949. Mammals of northern Colombia. Preliminary report no. 5: Bats (Chiroptera). Proceedings of the United States National Museum 99 (3246):429–454.
- Hewitt, G. M. 1988. Hybrid zones—natural laboratories for evolutionary studies. Trends in Ecology and Evolution 3:158–167.
- Hodell, D. A., J. H. Curtis, G. A. Jones, A. Higuera-Gundy, M. Brenner, M. W. Binford, and K. T. Dorsey. 1991. Reconstruction of Caribbean climate change over the past 10,500 years. Nature 352:790–793.
- Hoffmann, F. G., and R. J. Baker. 2001. Systematics of bats of the genus *Glossophaga* (Chiroptera: Phyllostomidae) and phylogeography in *G. soricina* based on the cytochrome-*b* gene. Journal of Mammalogy 82:1092–1101.
- Homan, J. A., and J. K. Jones, Jr. 1975. *Monophyllus plethodon*. Mammalian Species 58:1–2.
- Hood, C. S., and J. K. Jones, Jr. 1984. *Noctilio leporinus*. Mammalian Species 216:1–7.
- Husson, A. M. 1962. The bats of Suriname. Zoologische Monographien, Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands 2:xxxiv + 1–569.
- Issartel, G., and F. Leblanc. 2004. Contribution à l'inventaire des chiroptères de Martinique. Direction Régionale de l'Environnement, Martinique 63 pp.
- Jones, J. K., Jr. 1978. A new bat of the genus *Artibeus* from the Lesser Antillean island of St. Vincent. Occasional Papers, Museum of Texas Tech University 51:1–6.
- Jones, J. K., Jr. 1989. Distribution and systematics of bats in the Lesser Antilles. Pp. 645–660 in Biogeography of the West Indies: past, present, and future (C. A. Woods, ed.). Sandhill Crane Press, Inc., Gainesville, Florida.
- Jones, J. K., Jr., and C. J. Phillips. 1970. Comments on the systematics and zoogeography of the bats in the Lesser Antilles. Studies on the Fauna of Curaçao and Other Caribbean Islands 32:131–145.
- Jones, J. K., Jr., and C. J. Phillips. 1976. Bats of the genus *Stur-nira* in the Lesser Antilles. Occasional Papers, Museum of Texas Tech University 40:1–16.
- Jones, J. K., Jr., and A. Schwartz. 1967. Bredin-Archbold-Smithsonian Biological Survey of Dominica. 6. Synopsis of bats of the Antillean genus *Ardops*. Proceedings of the United States National Museum 124(3634):1–13.
- Jones, K. E., K. E. Barlow, N. Vaughan, A. Rodríguez-Durán, and M. R. Gannon. 2001. Short-term impacts of extreme environmental disturbance on the bats of Puerto Rico. Animal Conservation 4:59–66.

- Khan, F. A. A., C. D. Phillips, and R. J. Baker. 2014. Time-frames of speciation, reticulation, and hybridization in the bulldog bat explained through phylogenetic analyses of all genetic transmission elements. *Systematic Biology* 63:96–110.
- Koopman, K. F. 1968. Taxonomic and distributional notes on Lesser Antillean bats. *American Museum Novitates* 2333:1–13.
- Koopman, K. F. 1989. A review and analysis of the bats of the West Indies. Pp. 635–643 in *Biogeography of the West Indies: past, present, and future* (C. A. Woods, ed.). Sandhill Crane Press, Gainesville, Florida.
- Krutzsch, P. H., and D. W. Nellis. 2006. Reproductive anatomy and cyclicity of the male bat *Brachyphylla cavernarum* (Chiroptera: Phyllostomidae). *Acta Chiropterologica* 8:497–507.
- Kuo, H., S. Chen, Y. Fang, J. A. Cotton, J. Parker, G. Csorba, B. K. Lim, J. L. Eger, C. Chen, C., Chou, and S. J. Rossiter. 2015. Speciation processes in putative island endemic sister bat species: false impressions from mitochondrial DNA and microsatellite data. *Molecular Ecology* 24:5910–5926.
- Lack, D. 1976. *Island biology: illustrated by the land birds of Jamaica*. University of California Press, Berkeley and Los Angeles.
- Landsea, C. W., R. A. Pielke, Jr., A. M. Mestas-Núñez, and J. A. Knaff. 1999. Atlantic basin hurricanes: indices of climatic changes. *Climatic Change* 42:89–129.
- Lamas, C. J. E., S. S. Nihei, A. M. Cunha, and M. S. Couri. 2014. Phylogeny and biogeography of *Heterostylum* (Diptera: Bombyliidae): evidence for an ancient Caribbean diversification model. *Florida Entomologist* 97:952–966.
- Lamichhaney, S., F. Han, M. T. Webster, L. Andersson, B. R. Grant, and P. R. Grant. 2017. Rapid hybrid speciation in Darwin's finches. *Science* 359(6372):224–228.
- Larsen, P. A., S. R. Hofer, M. C. Bozeman, S. C. Pedersen, H. H. Genoways, C. J. Phillips, D. E. Pumo, and R. J. Baker. 2007. Phylogenetics and phylogeography of the *Artibeus jamaicensis* complex based on the cytochrome-*b* DNA sequence. *Journal of Mammalogy* 88:712–727.
- Larsen, P. A., M. R. Marchán-Rivadeneira, and R. J. Baker. 2010. Natural hybridization generates mammalian lineage with species characteristics. *Proceedings of the National Academy of Sciences* 107:11447–11452.
- Larsen, P. A., M. R. Marchán-Rivadeneira, and R. J. Baker. 2013. Speciation dynamics of the fruit-eating bats (genus *Artibeus*): evidence of ecological divergence in Central American populations. Pp. 315–339 in *Bat evolution, ecology, and conservation* (R. A. Adams and S. C. Pedersen, eds.). Springer, New York.
- Larsen, P. A., L. Siles, S. C. Pedersen, and G. G. Kwiecinski. 2011. A new species of *Micronycteris* (Chiroptera: Phyllostomidae) from Saint Vincent, Lesser Antilles. *Mammalian Biology* 76:687–700.
- Larsen, R. J., K. A. Boegler, H. H. Genoways, W. P. Masefield, R. A. Kirsch, and S. C. Pedersen. 2007. Mist netting bias, species accumulation curves, and the rediscovery of two bats on Montserrat (Lesser Antilles). *Acta Chiropterologica* 9:423–435.
- Larsen, R. J., P. A. Larsen, H. H. Genoways, F. M. Catzefflis, K. Geluso, G. G. Kwiecinski, S. C. Pedersen, F. Simal, and R. J. Baker. 2012. Evolutionary history of Caribbean species of *Myotis*, with evidence of a third Lesser Antillean endemic. *Mammalian Biology* 77: 124–134.
- Larsen R. J., P. A. Larsen, C. D. Phillips, H. H. Genoways, G. G. Kwiecinski, S. C. Pedersen, C. J. Phillips, and R. J. Baker. 2017. Patterns of morphological and molecular evolution in the Antillean tree bat, *Ardops nichollsi* (Chiroptera: Phyllostomidae). *Occasional Papers, Museum of Texas Tech University* 345:1–28.
- LaVal, R. K. 1973. Observations on the biology of *Tadarida brasiliensis cynocephala* in southeastern Louisiana. *American Midland Naturalist* 89:112–120.
- Lewis-Oritt, N., R. A. Van Den Bussche, and R. J. Baker. 2001. Molecular evidence for evolution of piscivory in *Noctilio* (Chiroptera: Noctilionidae). *Journal of Mammalogy* 82:748–759.
- Lindsay, K. C., G. G. Kwiecinski, S. C. Pedersen, J.-P. Bacle, and H. H. Genoways. 2010. First record of *Ardops nichollsi* from Antigua, Lesser Antilles. *Mammalia* 74:93–95.
- Lindsey, L. L., and L. K. Ammerman. 2016. Patterns of genetic diversification in a widespread species of bat, *Molossus molossus*. *Occasional Papers, Museum of Texas Tech University* 339:1–15.
- López-Wilchis, R., M. Flores-Romero, L. M. Guevara-Chumacero, A. Serrato-Díaz, J. Díaz-Larrea, F. Salgado-Mejía, C. Ibañez, L. O. Salles, and J. Juste. 2016. Evolutionary scenarios associated with the *Pteronotus parnellii* cryptic species-complex. *Acta Chiropterologica* 18:91–116.
- Lucek, K., A. Sivasundar, and O. Seehausen. 2012. Evidence of adaptive evolutionary divergence during biological invasion. *PLoS ONE* 7(11): e49377. doi:10.1371/journal.pone.0049377.
- MacArthur, R. H., and E. O. Wilson. 1963. An equilibrium theory of insular zoogeography. *Evolution* 17:373–387.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey.
- Macdonald, R., C. J. Hawkesworth, and E. Heath. 2000. The Lesser Antilles volcanic chain: a study in arc magmatism. *Earth-Science Reviews* 49:1–76.
- Marble, R. M. 1939. Yellow-billed tropic-bird in Vermont. Pg. 176 in *Hurricane Aftermath* (R.M. Marble, G. B. Hen-

- dricks, C. M. Meade, J. C. Dickinson, Jr., J. B. Calhoun, S. A. Eliot, Jr., and A. D. Cruickshank). *Auk* 56:176–179.
- McCain, C. M. 2005. Elevational gradients in diversity of small mammals. *Ecology* 86:366–372.
- McCarthy, T. J., and R. W. Henderson. 1992. Confirmation of *Ardops nicholli* on Marie-Galante, Lesser Antilles, and comments on other bats. *Caribbean Journal of Science* 28:106–107.
- McGuire, J. A., C. W. Linkem, M. S. Koo, D. W. Hutchinson, A. K. Lappin, D. I. Orange, J. Lemos-Espinal, B. R. Riddle, and J. R. Jaeger. 2007. Mitochondrial introgression and incomplete lineage sorting through space and time: phylogenetics of crotaphytid lizards. *Evolution* 61:2879–2897.
- McNab, B. K. 1969. The economics of temperature regulation in neotropical bats. *Comparative Biochemistry and Physiology* 31: 227–268.
- Miller, G. S., Jr. 1902. Twenty new American bats. *Proceedings of the Academy of Natural Sciences of Philadelphia* 54:389–412.
- Miller, G. S., Jr. 1906. Twelve new genera of bats. *Proceedings of the Biological Society of Washington* 19:83–86.
- Miller, G. S., Jr. 1913a. Five new mammals from tropical America. *Proceedings of the Biological Society of Washington* 26:31–34.
- Miller, G. S., Jr. 1913b. Revision of bats of the genus *Glossophaga*. *Proceedings of the Biological Society of Washington* 46:413–429.
- Muñoz-Romo, M., E. A. Herrera, and T. H. Kunz. 2008. Roosting behavior and group stability of the big fruit-eating bat *Artibeus lituratus* (Chiroptera: Phyllostomidae). *Mammalian Biology* 73:214–221.
- Owen, R. D., R. K. Chesser, and D. C. Carter. 1990. The systematic status of *Tadarida brasiliensis cynocephala* and Antillean members of the *Tadarida brasiliensis* group, with comments on the generic name *Rhizomops* Legendre. *Occasional Papers, Museum of Texas Tech University* 133:1–18.
- Pavan, A. C., and G. Marroig. 2016. Integrating multiple evidences in taxonomy: species diversity and phylogeny of mustached bats (Mormoopidae: *Pteronotus*). *Molecular Phylogenetics and Evolution* 103:184–198.
- Pavan, A. C., and G. Marroig. 2017. Timing and patterns of diversification in the Neotropical bat genus *Pteronotus* (Mormoopidae). *Molecular Phylogenetics and Evolution* 108:61–69.
- Pavan, A. C., F. M. Martins, and J. S. Morgante. 2013. Evolutionary history of bulldog bats (genus *Noctilio*): recent diversification and the role of the Caribbean in Neotropical biogeography. *Biological Journal of the Linnean Society* 108:210–224.
- Pedersen, S. C., H. H. Genoways, and P. W. Freeman. 1996. Notes on bats from Montserrat (Lesser Antilles) with comments concerning the effects of Hurricane Hugo. *Caribbean Journal of Science* 32:206–213.
- Pedersen, S. C., H. H. Genoways, G. G. Kwiecinski, P. A. Larsen, and R. J. Larsen. 2013. Biodiversity, biogeography, and conservation of bats in the Lesser Antilles. Pp. 62–73, 330 in *Biodiversité insulaire: la flore, la faune et l'homme dans les Petites Antilles* (J.-L. Vernier and M. Burac, eds.). Schoelchers, Martinique, Direction de l'Environnement, de l'Aménagement et du Logement de Martinique et Université des Antilles et de la Guyane, France.
- Pedersen, S. C., H. H. Genoways, M. N. Morton, J. W. Johnson, and S. E. Courts. 2003. Bats of Nevis, northern Lesser Antilles. *Acta Chiropterologica* 5:251–267.
- Pedersen, S. C., H. H. Genoways, M. N. Morton, G. G. Kwiecinski, and S. E. Courts. 2005. Bats of St. Kitts (St. Christopher), northern Lesser Antilles, with comments regarding capture rates of Neotropical bats. *Caribbean Journal of Science* 41:744–760.
- Pedersen, S. C., H. H. Genoways, M. N. Morton, V. J. Swier, P. A. Larsen, K. C. Lindsay, R. A. Adams, and J. D. Apino. 2006. Bats of Antigua, northern Lesser Antilles. *Occasional Papers, Museum of Texas Tech University* 249:1–18.
- Pedersen, S. C., G. G. Kwiecinski, H. H. Genoways, R. J. Larsen, P. A. Larsen, C. J. Phillips, and R. J. Baker. in press. Bats of St. Lucia, Lesser Antilles. *Special Publication, Museum of Texas Tech University*.
- Pedersen, S. C., G. G. Kwiecinski, P. A. Larsen, M. N. Morton, R. A. Adams, H. H. Genoways, and V. J. Swier. 2009. Bats of Montserrat: population fluctuations in response to hurricanes and volcanoes, 1979–2004. Pp. 302–340 in *Island bats: evolution, ecology, and conservation* (T. H. Fleming and P. A. Racey, eds.). University of Chicago Press, Chicago, Illinois.
- Phillipsborn, R. 1999. Perspective from a NOAA hurricane hunter. NOAA News Online Story Number 272. National Oceanographic and Atmospheric Administration. <http://www.noaa.gov/stories/s272.htm> (accessed 10 May 2018).
- Phillips, C. J., C. D. Phillips, J. Goecks, E. P. Lessa, C. G. Sotero-Caio, B. Tandler, M. R. Gannon, and R. J. Baker. 2014. Dietary and flight energetic adaptations in a salivary gland transcriptome of an insectivorous bat. *PLoS ONE* 9(1):e83512. doi:10.1371/journal.pone.0083512.
- Phillips, C. J., D. E. Pumo, H. H. Genoways, and P. E. Ray. 1989. Caribbean island zoogeography: a new approach using mitochondrial DNA to study Neotropical bats. Pp. 661–684 in *Biogeography of the West Indies: past, present, and future* (C. A. Woods, ed.). Sandhill Crane Press, Gainesville, Florida.
- Phillips, C. J., D. E. Pumo, H. H. Genoways, P. E. Ray, and C. A. Briskey. 1991. Mitochondrial DNA evolution and phylogeography in two Neotropical fruit bats, *Artibeus jamaicensis* and *Artibeus lituratus*. Pp. 97–123 in *Latin*

- American mammalogy, history, biodiversity, and conservation (M. A. Mares and D. J. Schmidly, eds.). University of Oklahoma Press, Norman.
- Porter, C. A., S. R. Hoofer, C. A. Cline, F. G. Hoffman, and R. J. Baker. 2007. Molecular phylogenetics of the phyllostomid bat genus *Micronycteris* with descriptions of two new subgenera. *Journal of Mammalogy* 88:1205–1215.
- Powers, L. V., S. C. Kandarian, and T. H. Kunz. 1991. Ontogeny of flight in the little brown bat, *Myotis lucifugus*: behavior, morphology, and muscle histochemistry. *Journal of Comparative Physiology A* 186:675–681.
- Pumo, D. E., E. Z. Golden, B. Elliot, C. J. Phillips, and H. H. Genoways. 1988. Mitochondrial DNA polymorphism in three Antillean island populations of the fruit bat, *Artibeus jamaicensis*. *Molecular Biology and Evolution* 5:79–89.
- Pumo, D. E., I. Kim, J. Remsen, C. J. Phillips, and H. H. Genoways. 1996. Molecular systematics of the fruit bat, *Artibeus jamaicensis*: origin of an unusual island population. *Journal of Mammalogy* 77:491–503.
- Redondo, R. A. F., L. P. S. Brina, R. F. Silva, A. D. Ditchfield, and F. R. Santos. 2008. Molecular systematics of the genus *Artibeus* (Chiroptera: Phyllostomidae). *Molecular Phylogenetics and Evolution* 49:44–58.
- Ricklefs, R. E., and E. Bermingham. 2004a. History and the species-area relationship in Lesser Antillean birds. *American Naturalist* 163:227–239.
- Ricklefs, R. E., and E. Bermingham. 2004b. Application of Johnson et al.'s speciation threshold model to apparent colonization times of island biotas. *Evolution* 58:1664–1673.
- Ricklefs, R. E., and E. Bermingham. 2008. The West Indies as a laboratory of biogeography and evolution. *Philosophical Transactions of the Royal Society of London B, Biological Sciences* 363(1502):2393–2413.
- Ricklefs, R. E., and I. J. Lovette. 1999. The roles of island area per se and habitat diversity in the species-area relationships of four Lesser Antillean faunal groups. *Journal of Animal Ecology* 68:1142–1160.
- Rodríguez-Durán, A., and T. H. Kunz. 2001. Biogeography of West Indian bats: an ecological perspective. Pp. 355–407 in *Biogeography of the West Indies: patterns and perspectives* (C. A. Woods and F. E. Sergile, eds.). CRC Press, Boca Raton, FL.
- Rodríguez-Durán, A., and R. Vazquez. 2001. The bat *Artibeus jamaicensis* in Puerto Rico (West Indies): seasonality of diet, activity, and effect of a hurricane. *Acta Chiropterologica* 3:53–61.
- Rojas, D., A. Vale, V. Ferrero, and L. Navarro. 2011. When did plants become important to leaf-nosed bats? Diversification of feeding habits in the family Phyllostomidae. *Molecular Ecology* 20:2217–2228.
- Sánchez-Cordero, V. 2001. Elevational gradients of diversity for rodents and bats in Oaxaca, México. *Global Ecology and Biogeography* 10:63–76.
- Santiago-Valentin, E., and R. G. Olmstead. 2004. Historical biogeography of Caribbean plants: introduction to current knowledge and possibilities from a phylogenetic perspective. *Taxon* 53:299–319.
- Schwartz, A. 1955. The status of the species of the *brasiliensis* group of the genus *Tadarida*. *Journal of Mammalogy* 36:106–109.
- Schwartz, A., and J. K. Jones, Jr. 1967. Bredin-Archbold-Smithsonian Biological Survey of Dominica. 7. Review of bats of the endemic Antillean genus *Monophyllus*. *Proceedings of the United States National Museum* 124(3635):1–20.
- Scott, J. A. 1972. Biogeography of Antillean butterflies. *Biotropica* 4:32–45.
- Seutin, G., N. K. Klein, R. E. Ricklefs, and E. Bermingham. 1994. Historical biogeography of the bananaquit (*Coereba flaveola*) in the Caribbean region: a mitochondrial DNA assessment. *Evolution* 48:1041–1061.
- Shamel, H. H. 1931. Notes on the American bats of the genus *Tadarida*. *Proceedings of the United States National Museum* 78(19):1–27.
- Siles, L., D. M. Brooks, H. Aranibar, T. Tarifa, V. M. R. Julieta, J. M. Rojas, and R. J. Baker. 2013. A new species of *Micronycteris* (Chiroptera: Phyllostomidae) from Bolivia. *Journal of Mammalogy* 94:881–896.
- Simberloff, D. S. 2009. The role of propagule in biological invasions. *Annual Review of Ecology, Evolution, and Systematics* 40: 81–102.
- Simmons, N. B. 2005. Order Chiroptera. Pp. 312–529 in *Mammal species of the world: a taxonomic and geographic reference*, 3rd ed. (D. E. Wilson and D. M. Reeder, eds.). John Hopkins University Press, Baltimore, Maryland.
- Smith, J. D. 1972. Systematics of the chiropteran family Mormoopidae. *Miscellaneous Publication of the Museum of Natural History, University of Kansas* 56:1–132.
- Soto-Centeno, J. A., and D. W. Steadman. 2015. Fossils reject climate changes as cause of extinction of Caribbean bats. *Scientific Reports* 5:1–7.
- Speed, R. C., P. L. Smith-Horowitz, K. V. S. Perch-Nielsen, J. B. Saunders, and A. B. Sanfilippo. 1993. Southern Lesser Antilles arc platform: pre-late Miocene stratigraphy, structure, and tectonic evolution. *Geological Society of America, Special Papers* 277:1–98.
- Steinbauer, M. J. 2016. A generalization of the taxon cycle. *Journal of Biogeography* 44:1110–1112.
- Swanepoel, P., and H. H. Genoways. 1978. Revision of the Antillean bats of the genus *Brachyphylla* (Mammalia:

- Phyllostomatidae). Bulletin of the Carnegie Museum of Natural History 12:1–53.
- Swanepoel, P., and H. H. Genoways. 1983. *Brachyphylla cavernarum*. Mammalian Species 205:1–6.
- Talbot, J. 1983. Cumberland hydroelectric project: environmental assessment. AID/RDO/C, Bridgetown, Barbados.
- Tavares, V. D. C., O. M. Warsi, F. Balserio, C. A. Mancina, and L. M. Dávalos. 2018. Out of the Antilles: fossil phylogenies support reverse colonization of bats to South America. Journal of Biogeography 45:859–873.
- Thoisy, B. d., A. C. Pavan, M. Delaval, A. Lavergne, T. Luglia, K. Pineau, M. Ruedi, V. Rufray, and F. Catzefflis. 2014. Cryptic diversity in common mustached bats *Pteronotus* cf. *parnellii* (Mormoopidae) in French Guiana and Brazilian Amapa. Acta Chiropterologica 16:1–13.
- Timm, R. M., and H. H. Genoways. 2003. West Indian mammals from the Albert Schwartz Collection: biological and historical information. Scientific Papers of the Natural History Museum, University of Kansas 29:1–47.
- Trejo-Torres, J. C., and J. D. Ackerman. 2001. Biogeography of the Antilles based on a parsimony analysis of orchid distributions. Journal of Biogeography 28:775–794.
- Tuck, L. M. 1968. Recent Newfoundland bird records. Auk 85:304–311.
- Twyford, A. D., and R. A. Ennos. 2012. Next-generation hybridization and introgression. Heredity 108:179–189.
- UNIDATA. 2017. Community hurricane preparedness: basic structure. Accessed at <<http://www.unidata.ucar.edu/data/NGCS/objects/chp/structure/>> on 2 July.
- USGS, Cascades Volcano Observatory. 2011. Accessed at <http://vulcan.wr.usgs.gov/Volcanoes/WestIndies/description_west_indies_volcanoes.html> 11 February.
- Valente, L., R. S. Etienne, and L. M. Dávalos. 2017. Recent extinctions disturb path to equilibrium diversity in Caribbean bats. Nature Ecology & Evolution 1:doi:10.1038/s41559-016-0026.
- Varona, L.S. 1974. Catálogo de los mamíferos vivos y extinguidos de las Antillas. Editorial Academica, Academia de Ciencias de Cuba La Habana.
- Vaughan, N. 1995. New records of bats on St. Vincent. Bulletin of the British Ecological Society 26:102–104.
- Vaughan, N., and J. E. Hill. 1996. Bat (Chiroptera) diversity and abundance in banana plantations and rain forest, and three new records for St. Vincent, Lesser Antilles. Mammalia 60:441–447.
- Vaughan Jennings, N., S. Parsons, K. E. Barlow, and M. R. Gannon. 2004. Echolocation calls and wing morphology of bats from the West Indies. Acta Chiropterologica 6:75–90.
- Velazco, P. M., and B. D. Patterson. 2013. Diversification of the yellow-shouldered bat, genus *Sturnira* (Chiroptera, Phyllostomidae), in the New World tropics. Molecular Phylogenetics and Evolution 68:683–698.
- Velo-Antón, G., K. R. Zamudio, and A. Cordero-Rivera. 2012. Genetic drift and rapid evolution of viviparity in insular fire salamanders (*Salamandra salamandra*). Heredity 108:410–418.
- Waide, R. B. 1991. The effect of Hurricane Hugo on bird populations in the Luquillo Experimental Forest, Puerto Rico. Biotropica 23:475–480.
- Walker, L. R. 1991. Tree damage and recovery from Hurricane Hugo in Luquillo Experimental Forest, Puerto Rico. Biotropica 23:379–385.
- Waters, J. M. 2011. Competitive exclusion: phylogeography's “elephant in the room”? Molecular Ecology 20:4388–4394.
- Watson, J., J. Spector, and T. Jones. 1958. Soil and land-use surveys, No. 3: St. Vincent. Regional Research Center, The Imperial College of Tropical Agriculture, University of the West Indies, St. Augustine, Trinidad.
- Webster, W. D. 1993. Systematics and evolution of bats of the genus *Glossophaga*. Special Publications, Museum of Texas Tech University 36:1–184.
- Webster, W. D., and C. O. Handley, Jr. 1986. Systematics of Miller's long-tongued bat, *Glossophaga longirostris*, with descriptions of two new subspecies. Occasional Papers, Museum of Texas Tech University 100:1–22.
- Webster, W. D., C. O. Handley, Jr., and P. J. Soriano. 1998. *Glossophaga longirostris*. Mammalian Species 576:1–5.
- Whittaker, R. J. 1998. Island biogeography: ecology, evolution, and conservation. Oxford University Press, New York and Oxford.
- Whittaker, R. J. 2000. Scale, succession and complexity in island biogeography: are we asking the right questions? Global Ecology and Biogeography 9:75–85.
- Wilder, J.A., and H. Hollocher. 2003. Recent radiation of endemic Caribbean *Drosophila* of the Dunni subgroup inferred from multilocus DNA sequence variation. Evolution 57:2566–2579.
- Wilkins, K. T. 1989. *Tadarida brasiliensis*. Mammalian Species 331:1–10.
- Williams, S. L., and H. H. Genoways. 2008. Subfamily Phyllostominae. Pp. 255–299 in Mammals of South America, vol. 1. (A. L. Gardner, ed.). University of Chicago Press, Chicago, Illinois.
- Williamson, M., and A. Fitter. 1996. The varying success of invaders. Ecology 77:1661–1666.
- Willig, M. R., S. J. Presley, C. P. Bloch, and H. H. Genoways. 2009. Macroecology of Caribbean bats: effects of area,

- elevation, latitude, and hurricane-induced disturbance. Pp. 216–264 in *Island bats: evolution, ecology, and conservation* (T. H. Fleming and P. A. Racey, eds.). University of Chicago Press, Chicago, Illinois.
- Wilson, D. E. 1973. Reproduction in Neotropical bats. *Periodicum Biologorum* 75:215–217.
- Wilson, D. E. 1979. Reproductive pattern. Pp. 317–378 in *Biology of bats of the New World family Phyllostomatidae, Part III* (R. J. Baker, J. K. Jones, Jr., and D. C. Carter, eds.). Special Publications, Museum of Texas Tech University 16:1–441.
- Wright, S. J. 1981. Intra-archipelago vertebrate distributions: the slope of the species-area relation. *American Naturalist* 118:726–748.
- Wunderle, J. M., Jr. 1985. An ecological comparison of the avifauna of Grenada and Tobago, West Indies. *Wilson Bulletin* 97:356–365.
- Yacoe, M. E., J. W. Cummings, P. Myers, and G. K. Creighton. 1982. Muscle enzyme profile, diet, and flight in South American bats. *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology* 242:R189–R194.
- Yannic, G., P. Basset, and J. Hausser. 2008. A hybrid zone with coincident clines for autosomal and sex-specific markers in the *Sorex araneus* group. *Journal of Evolutionary Biology* 21:658–667.

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APPENDIX

St. Vincent Gazetteer.—The coordinates for collecting sites that we visited during our survey were determined by using a Garmin eTrex® handheld GPS system. Coordinates for sites where other collectors conducted the work were taken from the specimens, published records, or other reference material, including online St. Vincent gazetteers.

Locality	Parish	Latitude	Longitude	Elevation (m)
Above Owia Big River Cave	Charlotte	13°22'10.7"N	61°08'57.1"W	172
Argyle	Charlotte	13°09'44.6"N	61°09'22.3"W	30
Arnos Vale Factory Ruins	St. George	13°08'47.8"N	61°12'42.7"W	18
Baleine Falls	St. David	13°22'13.6"N	61°11'36.2"W	122
Barrouallie	St. Patrick	13°14'09"N	61°16'19"W	15
Bat Cave	St. Andrew	13°11'10.6"N	61°16'15.2"W	3
Black Point Cave (Tunnel)	Charlotte	13°15'46.0"N	61°07'01.0"W	5
Botanical Garden	St. George	13°09'54.9"N	61°13'41.1"W	67
Brighton	St. George	13°07'52.7"N	61°10'28.3"W	76
Buccament River	St. Andrew	13°11'30.2"N	61°16'00.6"W	3
Calliagua	St. George	13°07'48.7"N	61°11'45"W	6
Cane Garden Point Cave	St. George	13°08'24.3"N	61°13'43.1"W	2
Chateaubelair Point Bat Hole	St. David	13°17'40.2"N	61°14'44.1"W	4
Clifton Hill	St. George	13°10'17.8"N	61°10'09.2"W	121
Colonarie River, at Morris Pasture	Charlotte	13°14'10.4"N	61°09'52.7"W	242
Convent, East Grove	St. Patrick	13°14'53.5"N	61°12'32.1"W	394
Cumberland Valley	St. Patrick	13°15'13.3"N	61°15'42.2"W	10
Dennis' Cave	St. George	13°08'16.9"N	61°13'36.0"W	2
Evesham	St. George	13°10'10.7"N	61°10'12.9"W	151
Fancy Trap	Charlotte	13°22'31.7"N	61°10'06.6"W	144
Golden Grove	Charlotte	13°11'58.3"N	61°11'32.7"W	426
Grand Sable Tunnel	Charlotte	13°16'18.3"N	61°07'42.6"W	99
Greiggs	Charlotte	13°13'18.2"N	61°10'42.7"W	443
Kings Hill	St. George	13°08'48.6"N	61°10'00"W	183
Kingstown	St. George	13°09'28"N	61°13'30"W	47
La Soufriere Trail	Charlotte	13°19'22.8"N	61°10'01.2"W	640
La Soufriere Trail Head	Charlotte	13°19'00.2"N	61°09'09.5"W	125
Lower Bellewood	St. Patrick	13°12'48.6"N	61°14'27.5"W	305
Lowrt [=Lowrey]	St. Andrew	13°12'54.3"N	61°13'10.8"W	305
Mesopotamia	Charlotte	13°10'0"N	61°10'0"W	93
Milikin Bay	St. George	13°07'59.3"N	61°10'03.5"W	11

Locality	Parish	Latitude	Longitude	Elevation (m)
Montreal	Charlotte	13°12'30.5"N	61°11'19.7"W	490
Morgan Woods	St. David	13°18'28.9"N	61°12'27.9"W	249
Mount Pleasant Ruins	St. George	13°09'03.4"N	61°09'13.9"W	88
Mt. St. Andrew 1	St. George	13°11'17.9"N	61°12'56.8"W	633
Mt. St. Andrew 2	St. Andrew	13°11'12.6"N	61°13'07.0"W	501
Mt. Wynne Bat Caves	St. Patrick	13°13'03.6"N	61°16'30.4"W	3
Old Sandy Bay	Charlotte	13°21'41.4"N	61°08'07.9"W	57
Owia Big River Cave	Charlotte	13°22'15.1"N	61°08'56.1"W	94
Parrot Lookout, Vermont Nature Trail	St. Andrew	13°13'20.2"N	61°12'43.4"W	484
Pembroke	St. Andrew	13°11'13.8"N	61°14'58.3"W	152
Perservance	Charlotte	13°16'38.7"N	61°08'52.0"W	744
Peruvian Vale	Charlotte	13°10'34.0"N	61°08'40.0"W	38
Ratho Mill	St. George	13° 07'46"N	61° 11'58"W	10
Richmond Hill	St. George	13°09'12.4"N	61°12'58.4"W	90
Rose Cottage	St. George	13°08'14.6"N	61°12'34.2"W	??
Rose Hall	St. David	13°15'46.9"N	61°13'35.4"W	379
Rose Hall, Lower End, Lower	St. David	13°15'51.2"N	61°13'25.7"W	377
Rose Hall, Lower End, Upper	St. David	13°15'58.3"N	61°13'21.9"W	435
Stubbs	St. George	13°08'45.4"N	61°09'31.6"W	7
Three River Ruins	Charlotte	13°14'52.2"N	61°08'13.2"W	93
Trail Head, Vermont Nature Trail	St. Andrew	13°12'58.8"N	61°12'53.4"W	304
Vermont	St. Andrew	13°12'13"N	61°13'27"W	123
Wallilabou	St. Patrick	13°14'54.2"N	61°16'09.1"W	10
Wallilabou River Falls	St. Patrick	13°14'54.2"N	61°15'37.7"W	46
Wallilabou River Gorge	St. Patrick	13°14'31.7"N	61°15'08.0"W	170
Waterworks	St. Andrew	13°12'55.6"N	61°12'52.0"W	305
Yambou River Gorge	Charlotte	13°10'16.8"N	61°09'14.8"W	46

